GENETIC AND ENVIRONMENTAL FACTORS AFFECTING SERUM MACROMINERALS AND PREWEANING GROWTH IN ANGUS, BRAHMAN AND THEIR CROSSES

BY

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Dedicated to

My late parents Absalom Odenya Oloo and Ducilla Mbayi Odenya who instilled within me the values to succeed in any endeavor

My wife Jemimah who patiently and lovingly provided support necessary for completion of this effort

My children Daniel, Patricia and Erick who encouraged and challenged me to finish my degree program

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GENETIC AND ENVIRONMENTAL FACTORS AFFECTING SERUM MACROMINERALS AND PREWEANING GROWTH IN ANGUS, BRAHMAN AND THEIR CROSSES

By

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Genetic and environmental factors affecting serum macrominerals and preweaning growth in beef cattle were investigated. Amounts of serum calcium, phosphorus, magnesium, potassium and sodium at weaning (WCa, WP, WMg, WK, WNa) and weaning weight (WW) were obtained from 380 Angus (A), Brahman (B) and A x B calves. Calves were produced by mating A, .75A.25B, .5A.5B, .25A.75B and Brangus sires to dams of the same breed groups except .25A.75B. The genetic effects model contained year, winter management, clean up herd, age of calf at first sampling, sex, age of dam and sex x age of dam interaction as fixed environmental effects. The genetic effects were the regressions on A sire additive, A x B direct nonadditive and A x B dam nonadditive. The variance components model contained all the above environmental effects plus the breed group of sire x breed group of dam interaction and the breed group of maternal grandsire x breed group of maternal granddam interaction as fixed genetic effects, and sire within breed group of sire as a random genetic effect. Year and sex were important for all traits ($P<.01$). Age of dam was important for WP and WMg ($P<.01$), WNa and WW ($P<.04$). Sex x age of dam interaction was important for WW ($P<.04$). Best Linear Unbiased Estimates of genetic effects that were significant ($P<.01$) were 1) -4.70 mg WCa, -3.00 mg WP, -.87 mg WMg, -11.58 mg WK, -108.35 mg WNa and -.38 kg WW for A sire additive, 2) -11.82 mg WP and .83 mg WMg for A dam additive, 3) 213.51 mg WCa, 81.19 mg WP, 48.26 mg WMg, 304.58 mg WK, 5931.66 mg WNa and 19.91 kg WW for nonadditive direct and 4) 366.56 mg WCa, 95.50 mg WP, 70.20 mg WMg, 550.72 mg WK, 9422.95 mg WNa and 36.31 kg WW for nonadditive maternal. The best combining ability was obtained by mating B sires to F_1 dams. Heritabilities were .39 (WCa), .40 (WP), .36 (WMg), .09 (WK), .46 (WNa) and .35 (WW). Genetic, environmental and phenotypic correlations were .66, .55, .57 (WCa, WP), .70, .71, .70 (WCa, WMg), 1.00, .86, .88 (WCa, WW), .86, .73, .75 (WMg, WW), 1.03, .65, .67 (WK, WNa), .94, .59, .62 (WK, WW) and .94, .84, .87 (WNa, WW). Serum WCa, WP, WMg and WNa could be useful in multiple trait genetic evaluation procedures to help identify animals that require low amounts of Ca, P, Mg and Na for preweaning growth. This may be advantageous in areas with these mineral deficiencies.

CHAPTER ONE
INTRODUCTION

Minerals are involved in the maintenance of normal growth and development, reproduction and health of animals. A large number of clinical disorders in farm animals are associated with deficiencies of minerals (Underwood, 1981; McDowell et al., 1983). The more common of these in farm animals are parturient paresis (milk fever) associated with calcium, rickets associated with calcium and phosphorus, hypomagnesemia (grass tetany) associated with magnesium, enzootic ataxia (swayback) associated with copper, and craving for salt associated with sodium and chlorine (Underwood, 1981). Deficiencies of these minerals also depress growth of animals (Minson, 1990). Thus, these minerals are of economic importance in animal production.

Most of these clinical disorders and depression of production (growth, reproduction) are more common in semi-tropical and tropical conditions than in temperate environments (McDowell et al., 1983). This mainly is because the soils in these areas are deficient in these elements (Minson, 1990). Thus, unless mineral supplements or supplementary feeds containing these minerals are included in their diets, animals will show deficiency disorders and reduction of full expression of their genetic potential. Despite supplementation, significant losses are experienced, possibly because the genetic mechanism underlying mineral metabolism is not well known (Wiener, 1984). Until the genetic basis is adequately understood, it is unlikely that it will be possible to formulate satisfactory predictions of the responses of animals to minerals in the diet. The application of such knowledge would be relevant to both intensive and extensive systems of animal production. On the other hand, it may be possible to formulate nutritional needs of animals more accurately in order to optimize production.

The production potential of an animal is regulated by both environment and heredity. Thus, if changes such as improvements in growth are desired, it is important to be aware of the contributions made by heredity, on the one hand, and the environment on the other. Without such information, any strategy for improvement will be ineffective or inefficient. Minerals play an important role in the animal's metabolism which in turn directly or indirectly affects the animal's phenotypic expression of economic traits, including growth. Thus, poor growth rates which may be attributed to mineral deficiency may be looked at as a subclinical production disease. The macrominerals including calcium, phosphorus, magnesium, potassium and sodium are among the elements that govern critical physiological functions. Although their concentration in the animal can be determined through other techniques, determination of mineral level in serum is advantageous because of accessibility without sacrifice of the animal.

There are indications that variations exist within and between blood metabolites including minerals (Rowlands and Manston, 1976). When concentrations of minerals are low in serum, there are frequently some animals which still maintain normal levels while others do not. The question arises, therefore, whether such animals with normal levels are endowed with a superior metabolism which enables them to cope under conditions that others find adverse, and whether such an ability to resist mineral deficiencies and to give high production levels can be identified from an animal's own level of serum mineral composition.

The occurrence of disorders and reduction of production due to inadequate body mineral levels in animals suggests that some animals are unable to meet their mineral requirements. The question arises whether such differences among animals are inherited and can be affected by selection.

The incidences of most of the metabolic disorders and depressed production are low and sporadic but expensive to reverse after occurring. Little progress can be expected in reducing the incidence of these metabolic disorders and depressed production in future generations by removing or allowing nature to remove only the clinically affected animals from the breeding population. Even such little change as might be expected from natural selection is counteracted by normal husbandry and veterinary practices which preserve deficient individuals by rescuing them from the consequences of metabolic disorders and depressed production.

Weaning weight is an important trait for selection in cow calf beef production systems because it provides an indication of the inherent potential of the calf to grow from birth to weaning. It also provides an indication of maternal environment that is provided by the dam to the calf. To the cow calf producer, weaning weight is particularly important since most calves are sold shortly after weaning and their weight determines the producer's income. Beef cattle producers recognize that calcium, phosphorus, magnesium, potassium and sodium are essential for the animal's growth (which in part is measured by weaning weight). Little work has been done on the inheritance of these macrominerals and how they relate to growth in beef animals. However, genetic progress in reducing metabolic disorders and depressed growth arising from mineral deficiency can only be made if the underlying variation is understood, measurable, and inherited. With the diversification and intensification of animal production systems to feed the growing world population (especially in developing countries), metabolic disorders and depression of growth are expected to increase in frequency; hence the need to address this problem.

Evaluation of breeds and animals should provide information on the full spectrum of biological traits needed to match their characteristics with production resources. If choices of breed groups are to be made in relation to their potential for use in breeding systems, each breed group needs to be evaluated for additive and nonadditive effects of genes on all traits important for economic production. Thus, the objectives of these studies were

i. to estimate additive and nonadditive group genetic effects of serum calcium, phosphorus and magnesium and weight at weaning in a multibreed herd of Angus, Brahman and their crosses,
ii. to estimate heritabilities of and genetic, environmental and phenotypic correlations among serum calcium, phosphorus, and magnesium and weight at weaning in a multibreed herd of Angus, Brahman and their crosses,
iii. to estimate additive and nonadditive group genetic effects of serum potassium and sodium and weight at weaning in a multibreed herd of Angus, Brahman and their crosses, and
iv. to estimate heritabilities of and genetic, environmental and phenotypic correlations among serum potassium and sodium and weight at weaning in a multibreed herd of Angus, Brahman and their crosses.

CHAPTER TWO
LITERATURE REVIEW

Sources of Variation of Macromineral Concentration

Environmental Factors

Age of animal. Serum macromineral concentrations tend to decrease with age. Kitchenham et al. (1975) reported that serum Mg concentrations in cattle tend to decrease with age at an estimated average rate of fall of about .010 mmol. per liter per year. This may be because of decreased absorption of minerals with age (Gibson, 1990). In a study done by Rusoff et al. (1951) in Louisiana, the authors reported the mean monthly serum P to be 29% higher in five-month old Sindhi-Jersey daughters than in their 42-month old dams. However, when deficiency exists, younger animals tend to suffer more than older animals. Rook and Storry (1962) indicated that about 30% of skeletal Mg can be mobilized and translocated to other areas of the body for such processes as soft tissue growth when Mg is highly deficient in calves whereas only 2% is extracted by mature animals (over five years old) to satisfy physiological needs.

Mineral content of diet. A significant decline in serum Ca occurs in response to a dietary deficiency of Ca (Underwood, 1981). Devlin et al. (1969) conducted two feeding trials to study the dietary K requirement of finishing steers. The K levels fed in the first study were .27%, .51%, .72% and .85%, and in the second trial the levels were .36%, .50%, .67% and .77%. The serum concentration increased as ration K increased, but the lowest ration K level was the only one resulting in significantly different serum K values.

Climate, season and stage of plant maturity. Plants mature in response to external factors which include climate and season (Underwood, 1981). This is reflected in serum concentration of minerals in animals.

Phosphorus, Mg, K, but not Ca content of forage plants decline markedly with advancing maturity (Underwood, 1981). Studies done by Espinoza et al. (1991) in forage plants of central Florida in 1987 and 1988 indicated year effects to be significant in Ca and Na. Concentrations of Ca, Mg, K, P and Na were below critical levels during winter thus suggesting deficiencies of these minerals. Rook and Storry (1962) reported a fall of serum Mg in beef herds on pasture during winter season which was attributed to nutritional deficiency resulting from a combination of low intake and poor absorption of Mg and probably also because of a low plane of energy nutrition. Payne and Payne (1987) reported that Na is low in summer pastures and is reflected in serum concentration of the element.

Sex. Females have slightly lower concentrations (8.8-10.2 mg per deciliter) than males (9.2-10.6 mg per deciliter) (Gibson, 1990). This might be because of serum albumin that is higher in females. In the case of Ca levels in females, the Ca concentration may be lower than that of males because of inhibitory effect of estrogen on Ca (Gibson, 1990).

Production level and physiological state. Macromineral requirements are dependent on the level of productivity and physiological state of the animal (NRC, 1976). Thus, if the requirements are not met, the animals will show low macromineral levels in the serum.

Rapidly growing young animals will show low concentration of macrominerals in serum when fed diets that are deficient in the macrominerals because of high requirements for growth (Underwood, 1981). Similarly, lactation draws heavily on body macrominerals (Ca, P, Mg, Na) because these macrominerals are used in milk synthesis (Underwood, 1981). Thus, a high yielding cow in lactation will show a lower concentration of the macrominerals than a low yielding one (Payne and Payne, 1987).

Gibson (1990) reported that serum Ca decreases by 5 to 6% up to the end of the third trimester of pregnancy, after which concentrations rise. Wilson et al. (1977) reported that serum P concentration decreases prior to parturition, with the lowest point being at the time of calving.

Other factors affecting mineral concentrations. Increased storage time and/or temperature postsampling tend to increase mineral serum concentrations, especially that of P. Burdin and Howard (1963) reported an increase of 64% in organic P during one week storage at ambient temperature as compared to only 4% increase when stored at 4^0 C for 12 days. This increase in

P is due to hydrolysis of organically bound P from phosphoric acid esters (Burdin and Howard, 1963). Forar et al. (1982) suggested that time of sampling should be standardized when collecting blood samples to reduce the effect of diurnal variation in serum P concentration in cattle.

Gibson (1990) reported that low serum Ca can occur following interference with Ca absorption. This might be attributed to factors like worm infestation (e.g. P absorption, Cohen, 1975).

Genetic Factors

Differences between breeds. Breed differences on mineral concentrations which depict requirements in animals have been reported. In a study which utilized Scottish Blackface, South Country Cheviot, Welsh Mountain sheep breeds and their F_2 crosses, Wiener and Field (1969) reported the ranking of copper blood concentration from the highest to lowest to be Blackface, Cheviot and Welsh breeds. The F_2 crossbreds had higher concentrations than the purebreds, thus indicating heterosis. Under tropical conditions, temperate breeds of cattle tend to lose substantial amounts of minerals (Underwood, 1981). This was supported by Payne et al. (1970) who reported that unacclimatized temperate cattle sweat profusely and lose saliva and mucous from the mouth, thus losing a significant amount of minerals. This could indicate that temperate breeds may have higher mineral requirements than tropical breeds when exposed to tropical conditions, if the temperate breeds are not adapted to such conditions. Comparing Merino and Lebanese fat-tailed sheep, Evans

(1954) reported that the majority of the Merino sheep appeared to have low potassium levels, whereas the Lebanese fat-tailed tended to have higher levels of potassium and sodium (Kerr, 1937). Fat-tailed sheep usually are dominant in semi-arid and arid conditions where there is stress of high temperature and poor quality feeds. Thus, higher levels of potassium and sodium may serve as biological indicators of adaptability in stressful semi-arid and arid environments.

Differences within breeds. Very little work has been done in this area, especially with cattle. However, the scanty literature available indicates that there is variation of mineral concentration within breeds.

There is evidence of animal variation within breeds for the efficiency of absorption of minerals from the diet which is reflected in mineral concentration (blood, serum, plasma). Field (1981) reported 3% to 35% variation in efficiency of absorption of magnesium in dairy cattle and 40% to 80% variation for absorption of phosphorus in sheep. Based on variable number of offspring of 10 different bulls (from 7 to 23 progeny per bull), Payne et al. (1970) reported that magnesium concentrations for sire progeny groups ranged from 2.2 to 2.9 mg per 100 ml plasma. Payne et al. (1970), however, did not indicate whether the variation among sires was statistically significant. Within the Scottish Blackface breed of sheep, Evans and King (1955) found potassium concentration in blood to fall distinctly into two types: animals with high levels(30-45 m.equivalent per liter) and those with low levels (10-20 m.equivalent per liter). In India, Sengupta (1974b) studied red cell electrolyte distribution in zebu cattle (Hariana and Sahiwal). He reported that the lowest K concentration was predominant in the Sahiwal breed (mean = 12.5 m.equivalent per liter). The highest concentration was predominant in the Hariana breed (38 m.equivalent). The animals with the lowest K concentration also had significantly higher packed cell volume, hemoglobin, red blood cell counts, and lower rectal temperatures indicating less thermal stress. Khattab et al. (1964) reported higher packed cell volume in low potassium groups in Welsh Mountain sheep. In contrast, Taneja et al. (1971) observed significantly higher packed cell volume, red blood cells and hemoglobin concentration in high potassium type Marwari sheep than in the low potassium type.

Inheritance of Minerals

Very little is known about inheritance of minerals. However, from a few studies, it would appear that the mode of inheritance may be different for each element. For example, Rowlands and Manston (1976) reported heritability estimates of blood calcium, magnesium, sodium and potassium to be .19, .21, .09, and .49, respectively, when determined by half-sib analysis of variance in the blood of 231 Hereford-Friesian calves from 12 sires. In another study in India, Sengupta (1974a) studied the inheritance of red cell K in buffaloes (Murah, Bhadawari breeds). He reported the inheritance of K in red blood cells to be controlled by a single pair of genes. The high K animals (87-91 m.equivalent per liter) were homozygous for the recessive allele while the low animals (37-41 m.equivalent per liter) represented the heterozygotes and also homozygotes for the other allele. The frequency of the recessive gene was .78 and .74 in the Murah and Bhadawari breeds respectively.

Relationship Between Mineral Concentration and Growth

There may be some association between certain mineral concentrations and growth. Sengupta (1974a) reported that Murah buffaloes with low potassium in the red cells had higher body weights than those with high potassium levels. Similar results were reported by Evans and Turner (1965) who found a significant phenotypic negative correlation between erythrocyte potassium concentration and body weight in F_2 Brahman-Shorthorn crossbreds. In the same experiment a significant negative correlation was found between erythrocyte sodium concentration and summer weight gain.

Calcium

Introduction

Calcium (Ca) is the most abundant mineral in the body (Underwood, 1981; NRC, 1984). About 99% of Ca is found in bones and teeth, and 1% is widely distributed in soft tissues and fluids (Underwood, 1981; McDowell et al., 1983). Cattle contain approximately 12 g Ca per kilogram liveweight (Minson, 1990). Calcium occurs as a free ion, bound to serum proteins and complexed to organic and inorganic acids (Underwood, 1981). Approximately 45 to 50% of the total serum Ca is bound to plasma proteins, principally albumin, and another 5 to 10% is complexed to anions, mainly citrate (Kukreja and

Abramson, 1982). Ionized Ca is the essential element for physiological functions (Underwood, 1981). Only .33% Ca is present in blood, with .30% in the plasma and .03% in the red blood cells (Minson, 1990).

Physiological Functions

Protein synthesis and growth

Calcium stimulates leucine incorporation into protein during incubations of sections of cell free preparations of the rat adrenal (Farase, 1971a; Farase, 1971b). Like adrenocorticotrophic hormone (ACTH) action, Ca enhances the transfer of amino acid from aminoacyl-tRNA to protein. Since ACTH increases the adrenal uptake of Ca, Ca may be responsible for the activation of the transfer enzymes by ACTH (Farese, 1971a). Conceivably, this may be the initial or early step whereby ACTH stimulates adrenal growth, since the early in vitro effect of ACTH on leucine incorporation in adrenal sections depends upon Ca. Since cyclic adenosine monophosphate (cAMP) also has Ca-dependent stimulatory effects on adrenal protein synthesis, it is possible that this nucleotide is ultimately responsible for Ca-mediated stimulation of adrenal protein synthesis by ACTH (Farese, 1971a). Depletion of intracellular Ca stores is accompanied by a concomitant four to ten fold reduction in the rate of amino acid incorporation (Brostrom and Brostrom, 1990). In studies of translation in intact GH_3 pituitary cells, Ca depletion with EGTA resulted in the disappearance of polysomes and an accumulation of 80S monosomes and ribosomal subunits typical of slowed rates of initiation of protein synthesis (Brostrom and

Brostrom, 1990). Calcium repletion rapidly restored cellular polysomal contents with an accompanying accumulation of 43S preinitiation complex (40S.eIF-2.Met-tRNA$_f$.GTP). This initiation process is activated by protein calmodulin (Darnell et al., 1990) and through the Ca dependent 1,2-Dioacylglycerol activate the protein kinase C (Darnell et al., 1990). The protein kinase C has specificity for serine and threonine residues on protein substrates. By this mechanism, protein kinase C is thought to act as a pathway for olypeptide growth factor. A rise in blood Ca levels triggers the release of insulin (Darnell et al., 1990) and elevates muscle protein synthesis in skeletal muscle (Goll et al., 1989). The growth promoting effects of insulin may be mediated by the receptor of insulin-like growth factor 1 (IGF-1). The IGF-1 stimulates differentiation of muscle cells through increased myogenic gene expression (Florini et al., 1991). Lehninger (1984) also reported that secretion of insulin requires Ca. Horowitz and Weinstein (1983) reported that Ca plays an important role in modulating growth of normal fibroblasts and epithelial cells. Normal cells exhibit negligible or limited growth in media containing low Ca concentrations (.001-.01mM rather than 1.25 mM). Following thermal stress at 46°C or chemical stress from exposure to sodium arsenite or 8-hydroxyquinoline, rates of amino acids incorporation in Ca-restored GH$_3$ cells were reduced acutely to those of unstressed Ca-depleted control preparations (Brostrom et al., 1989). Overall responses to heat or chemical stress appear to include acute destruction of Ca-stimulated initiation process of protein synthesis and slowed peptide chain elongation. Thus, it is conceivable that stress promotes uncoupling of Ca stores from translational activity.

Calcium also is needed for bone formation and teeth development (Underwood, 1981; McDowell et al., 1983). Bone formation is carried out by active osteoblasts which synthesize and extrude collagen into the adjacent extracellular space (Berne and Levy, 1988). The collagen fibrils line up and produce an organic matrix, osteoid within which Ca is then deposited as calcium phosphate ($Ca_3(PO_4)_2$ and hydroxyapatite $Ca_{10}(PO_4)_6(OH)_2$ (Harrison, 1984; Arnaud and Sanchez, 1990). The mineralization process requires normal plasma concentrations of Ca and phosphate and is dependent on vitamin D (Berne and Levy, 1988). Bone formation is stimulated by the hormones: somatomedins, insulin, and androgens and is inhibited by cortisol and parathyroid hormone (PTH). Bone resorption is stimulated by the hormones: parathyroid hormone, thyroid, cortisol, prostaglandins, lymphokines and vitamin D and is inhibited by calcitonin and estrogen hormones (Berne and Levy, 1988). Calcium balance reflects the degree of coupling of bone formation and resorption. Negative balances are experienced when bone resorption exceeds formation, and positive balances are experienced when bone formation exceeds bone resorption (Arnaud and Sanchez, 1990). The Ca that is present in bone acts as a reserve which can be drawn on to maintain a relatively uniform level of Ca in the blood supplying the tissue of the animal (Minson, 1990).

Other Functions

Calcium also participates in several enzymatic reactions and is of fundamental importance to all biological systems (Berne and Levy, 1988). It is a vital component in the mechanism of hormone secretion and a mediator of hormonal effects. Calcium is involved in neurotransmission, muscle contraction, and in blood coagulation. Thus, it is vital that cells be bathed with fluid in which Ca concentration is kept within the narrow limits of physiological tolerance (Berne and Levy, 1988).

Homeostasis

Calcium homeostasis is the result of an interplay of intestinal Ca absorption, skeletal Ca deposition and resorption and renal Ca excretion. Less than 1% of total body Ca is contained in the intravascular, intracellular, and interstitial fluids (Kukreja and Abramson, 1982). This small component of total body Ca is crucial to normal physiologic functions. The circulating level of Ca is kept in a fairly narrow range between 8.5 and 10.% mg/dl. Calcium is regulated by several hormones in the body. The role of these hormones in relationship to growth and development is reviewed below.

Parathyroid Hormone. The major hormone that regulates Ca metabolism is parathyroid hormone (PTH) (Parsons, 1979). Parathyroid Hormone (PTH) is secreted by the parathyroid glands which are located in the posterior aspect of the thyroid gland (Darnell et al., 1990). Parathyroid Hormone exerts its major effects by increasing bone resorption and Ca absorption. Parathyroid Hormone also stimulates the 1-hydroxylase activity of the kidney for 25-hydroxy-vitamin D, resulting in increased production of the active metabolite 1,25-dihydroxy-vitamin D [1,25(OH_2)-D]. This active metabolite in turn increases gastrointestinal absorption of Ca. At the renal level, PTH results in increased reabsorption of Ca. Hypercalcemia is observed in states of excessive PTH production, such as primary hyperparathyroidism (Berne and Levy, 1988).

The major control of intestinal Ca absorption is 1,25-$(OH)_2$D, which acts on intestinal Ca transport mechanisms (Berne and Levy, 1988). The synthesis of this metabolite is controlled by serum Ca and P. Hypocalcemia and hypophosphatemia result in increased production of 1,25-$(OH)_2$D which in turn results in increased Ca absorption (Berne and Levy, 1988). In addition to increasing the gastrointestinal absorption of Ca, this metabolite also has potent bone resorbing activity; excessive amounts of this compound cause hypercalcemia (Raisz et al., 1972).

Extracellular concentration of ionized Ca (e.g. plasma Ca) regulates parathyroid synthesis and secretion (Borle, 1974; Berne and Levy, 1988). The PTH hormone and the Ca ion form a negative feedback pair. Secretion of PTH is inversely related to the plasma Ca concentration in a sigmoidal fashion (Berne and Levy, 1988). Maximum secretory rates are achieved below a Ca concentration of 7 mg/dl. As Ca concentration increases to 11 mg/dl, PTH secretion is progressively diminished. Above 11 mg/dl there is a persistent basal rate of PTH secretion that is not suppressible by further elevation of plasma Ca. Prolonged exposure to a high ambient Ca concentration depresses the rate of PTH synthesis; the exact control point is not known (Berne and Levy, 1988). Calcium stimulates the intraglandular degradation of PTH. The net effect of increasing ambient Ca is to decrease both the glandular stores and release rates of PTH. Conversely, hypocalcemia increases PTH stores and secretory rates, and ultimately stimulates hyperplasia of the PTH glands as well (Berne and Levy, 1988).

The high levels of l,25-$(OH)_2$-D sharply decreases the level of prepro-PTH messenger RNA and eventually reduces the secretion of PTH. Epinephrine, a catecholamine hormone, stimulates PTH secretion through its β-adrenergic receptor, probably by activating adenylate cyclase (Berne and Levy, 1988). Calcitonin also stimulates PTH secretion (Berne and Levy, 1988) possibly by depression of adenyl cyclase that would in turn lead to an increased cyclic AMP concentration and an increased PTH secretion (Berne and Levy, 1988).

High concentrations of cyclic AMP stimulate release of cyclic AMP and the secretion of PTH in the medium by parathyroid glands in vitro (Abe and Sherwood, 1972).

Calcitonin. Calcitonin hormone (CT) is produced by the thyroid C or parafollicular cells and causes a decrease in bone resorption (Kukreja and Abramson, 1982) and subsequent lowering of plasma Ca (Berne and Levy, 1988). The major stimulus to secretion of calcitonin is a rise in plasma Ca. Binding of CT to plasma membrane receptors is followed by an elevation of the intracellular cAMP level (Berne and Levy, 1988). This cAMP initiates at least a portion of CT action in all target cells. Sequestration of Ca in the mitochondria, thus lowering cytosol Ca concentration, has been advanced as a mechanism for reducing the efflux of Ca from bone cells into the extracellular fluid (Berne and Levy, 1988). The effect of CT administration is a rapid fall in plasma Ca levels. The magnitude of this decrease is directly proportional to the baseline rate of bone turnover. Thus, young growing animals are most affected, whereas in adults, who have more stable skeletons, only minimal response is seen (Berne and Levy, 1988). In hypocalcemic conditions, inhibition of osteolysis by osteocytes and inhibition of bone resorption by osteoclasts are observed (Berne and Levy, 1988).

Vitamin D. There are two sources of vitamin D: 1) that produced in the skin from an inactive precursor, 7-Dehydrocholesterol by reactions that are promoted by exposure to the ultraviolet component of sunlight, and 2) that ingested in the diet from plants (vitamin D_2 or ergocalciferol). Vitamin D is not a classic hormone of endocrine origin, but its intimate and hormonelike relationship with Ca and phosphate metabolism and its mechanism of operation are similar to that of the steroid hormones, thus justifying it as a hormone (Berne and Levy, 1988). Vit D_2 differs from Vit D_3 in having an additional double bond at the 21 to 22 position but has the same biological actions to Vitamin D_3 for most species. Thus, the form Vitamin D is used to indicate both forms.

Under the influence of light (irradiation of epidermis of skin) 7-Dehydrocholesterol is photoconverted to vitamin D_3 cholecalciferol. Because of its fat solubility, absorption of the vitamin from the gut is mediated by bile salts and occurs via the lymphatic glands (Berne and Levy, 1988). After absorption by the intestine, all forms of vitamin D are converted to 25-hydroxycholecalciferol [25-(OH)D_3] in a reaction dependent on NADPH and oxygen (Borle, 1974; Lehninger, 1984). When vitamin D is deficient, 25-hydroxylation is enhanced (Berne and Levy, 1988). The 25-(OH)D_3 is the major metabolite circulating in the blood, bound to an α_2-globulin (Winter, 1972); however, it is not the ultimate physiological metabolite. From the liver, 25-(OH)D_3 is transported to the kidney where it is converted to 1,25-dihydroxycholecalciferol 1,25-$(OH)_2D_3$ if blood Ca levels are low. It is catalyzed in the mitochondria by the enzyme 25-(OH)D_3-1-hydroxylase (Gray et al., 1971). The reaction requires NADPH, flavoprotein, cytochrome P-450, and oxygen (Berne and Levy, 1988). Parathyroid hormone activates the enzyme and stimulates the reaction (Lehninger, 1984). The conversion of 1,25-$(OH)_2D_3$ has been shown to be inversely related to the plasma concentrations of inorganic phosphate (Borle, 1974). Low plasma phosphate stimulates 1,25-$(OH)_2D_3$ conversion, while at high plasma phosphate concentrations, 25-$(OH)_2D_3$ is converted into an inactive metabolite 24,25-$(OH)_2D_3$ (Borle, 1974). The primary effect of 1,25-$(OH)_2D_3$ is absorption of Ca in the intestine and promotion of Ca removal from bone.

Endocrine control of vitamin D actions occurs through regulation of renal 1-hydroxylase and 24-hydroxylase activities. The 25-OH-D_3 compound is preferentially directed toward the highly active metabolite 1,25-$(OH)_2$-D_3 whenever there is lack of Ca or lack of phosphate (Berne and Levy, 1988). In vitamin D-deficient states it may be partly the lack of 1,25-$(OH)_2D_3$ itself that enhances 1-hydroxylation, since 1,25-$(OH)_2D_3$ is a suppressor of 1-hydroxylase activity (Berne and Levy, 1988). When vitamin D is sufficient, the 1-hydroxylase enzyme also is subject to regulation by Ca and phosphate. Calcium deprivation leads to hypocalcemia, which in turn stimulates PTH secretion. The lowered plasma Ca and the elevated PTH concentration each independently stimulates 1-hydroxylase activity. Deprivation of phosphate leads to hypophosphatemia and directly to an increase in 1-hydroxylase activity (Berne and Levy, 1988). Vitamin D sufficiency, via 1,25-$(OH)_2$-D_3, and normal or high Ca and phosphate concentrations all stimulate the synthesis of 24,25-$(OH)_2$-D_3 which is considered to be an excretory product in vitamin D metabolism.

Absorption

Calcium ions are mainly absorbed by the intestine (McDowell et al., 1983; Berne and Levy, 1988; Arnaud and Sanchez, 1990). The ability of the intestine to absorb Ca is regulated by PTH, 1,25-$(OH)_2$-D_3 and CT. Animals receiving a Ca-deficient diet increase their ability to absorb Ca, while animals receiving high Ca diets absorb less Ca (NRC, 1984; Berne and Levy, 1988). Absorption is also increased during pregnancy and lactation (Care et al., 1980).

Absorption is stimulated by vitamin D and PTH (NRC, 1984; Berne and Levy, 1988).

The solubility of Ca compounds which affects this absorption is favored by acid conditions and hindered by alkaline conditions (NRC, 1984). Calcium absorption is greater in young than old animals (NRC, 1984). This could partly be because of milk that provides large quantities of Ca and at the same time also provides lactose which stimulates Ca absorption (White et al., 1968). The presence of sugars, lysine or arginine also enhance Ca absorption (White et al., 1968).

Vitamin D in the form of 1,25-$(OH)_2D_3$ is the physiologic and metabolically active metabolite controlling intestinal Ca absorption (Borle, 1974). Vitamin D may stimulate each phase of absorption of Ca ions by the epithelium of the small intestine through passage across the brush border membrane, traversal of the cytosol, and active extrusion across the basolateral membrane (Berne and Levy, 1988). Vitamin D_3 induces the synthesis of the cytosolic CaBP. The CaBP level correlates well with the capacity of the small intestine to absorb Ca (Berne and Levy, 1988). Vitamin D also increases the level of the intestinal membrane CaBP that may be involved in transporting Ca across the brush border plasma membrane. In addition, Vit D increases the level of basolateral Ca^{++}-ATPase that actively pumps Ca out of the enterocyte (Berne and Levy, 1988).

From nutritional standpoint, the intestinal absorption of Ca presents a major problem, largely because of the insolubility of most of Ca salts (White et al., 1968). In increasing order of solubility, the three forms of calcium phosphate are $Ca_3(PO^4)_2$, $CaHPO_4$ and $Ca(H_2PO_4)_2$. Only 30 to 50% of ingested Ca is normally absorbed (Arnaud and Sanchez, 1990).

Requirements

Adequate Ca nutrition depends not only on sufficient total dietary supplies, but also on the chemical forms in which they occur in the diet (Underwood, 1981; McDowell et al., 1983). The dietary Ca:P ratio also can be important (Underwood, 1981, McDowell et al., 1983). Liberal supplies of Vitamin D reduce the significance of adverse Ca:P ratios and enable the animal to make the best use of limited intakes of the minerals (Underwood, 1981). A dietary Ca:P ratio between 1:1 and 2:1 is assumed to be ideal for growth and bone formation since this is approximately the ratio of the two minerals in bone (Underwood, 1981; McDowell et al., 1983).

Beef cattle Ca requirements of .43 to .70% Ca are adequate for growing and fattening of steers and heifers (Underwood, 1981; McDowell et al., 1983).

Phosphorus

Introduction

Phosphorus (P) has long been recognized as a major essential macromineral for ruminants. However, many of the world's soils are derived from parental material which is low in P. Soils of low P support early maturing grass dominant pastures with a short summer growth period and hence a lengthy period of senescence (Cohen, 1980). Phosphorus in these grasses may be as low as .2 g P kg^{-1} organic matter during senescence and may reach only 1.5 g P kg^{-1} organic matter during the active growth period (Cohen, 1980). Such pastures are grazed by many of the world's livestock, particularly in developing countries (Underwood, 1981; McDowell et al, 1983). Although widely distributed in nature, P is not found in a free elemental state but in the phosphate form.

Physiological Functions

Protein synthesis and growth

Phosphorus functions as a component of nucleic acids, which are essential in cell growth and differentiation (Underwood, 1981). Nucleic acids are comprised of 10.0% P in DNA and 9.6% in RNA (Durand and Kawashima, 1980). The decoding of the codons in mRNA occurs in three phases, each utilizing different soluble factors that catalyze specific interactions among the large number of components that participate in protein synthesis. The three phases are initiation, elongation, and termination. The initiation process involves GTP, ATP, a number of initiation factors (eIF$_s$) mRNA, and ribosomal subunits, to form an 80S initiation complex (Darnell et al., 1990). The 80S initiation codon of initiator Met-tRNA$_f$, free of initiation factors, is then ready to decode all of the meaningful internal codons in the mRNA cistron.

Peptide chain elongation which serves to translate the internal codons between the initiation and termination requires GTP and elongation factors (EF$_s$) (Lehninger, 1984; Moldave, 1985). The elongation reactions, binding of appropriate aminoacyl -tRNA to the ribosomal A (acceptor) site, transpeptidation to form a peptide bound between the incoming aminoacyl moiety and methionyl (or peptidyl) residue at the P (donor) site, and movement of the ribosome on mRNA, are repeated until a termination code enters the A site (Moldave, 1985).

The sites of protein synthesis are the ribosomes (Darnell et al., 1990). The genetic information is brought to the ribosomes by RNA. There are inherent differences in the fractional rates of protein synthesis (Reeds, 1989). These differences relate primarily to the number of ribosomes (generally inferred from the RNA concentration) per cell (Reeds, 1989). The RNAs are synthesized from four ribonucleoside triphosphates (whose primary structure consist of adenine, cytosine, guanine, uracil) with the presence of DNA and magnesium ions and is catalyzed by DNA dependent RNA polymerase enzyme (White et al., 1968; Darnell et al., 1990). The termination phase of protein synthesis, when the A (decoding) site on the ribosome contains a termination codon, requires GTP and a specific protein factor (RF) (Moldave, 1985). The GTP-dependent, codon-specific binding of the termination factor to the ribosomal A site results in the hydrolysis of the peptidyl-tRNA ester at the P sites and release of the completed polypeptide chain (Moldave, 1985). Protein synthesis can be controlled by regulating the rate of formation of mRNA (White et al., 1968).

Cattle contain approximately 6.3 g P per kg liveweight (ARC, 1965). Approximately 80% of the P in the body is present in bone (ARC, 1965) with less than .4% in the serum. It is deposited in bone as calcium hydroxyapatite $[Ca_{10}(PO_4)_6(OH)_2]$ (NRC, 1984; Arnaud and Sanchez, 1990).

Other Functions

Phosphate is an integral component of all glycolytic compounds from glucose to pyruvate (Lehninger, 1984). These phosphate groups have three functions (Lehninger, 1984):

1. The phosphate groups are completely ionized at pH 7, thus giving each of the intermediates of glycolysis a net negative charge. Since cell membranes are generally impermeable to molecules having an electric charge, the glycolytic intermediates cannot escape from the cell.
2. They are essential components in the enzymatic conservation of metabolic energy since they are ultimately transferred to ADP to yield ATP.

3. The phosphate groups serve as recognition or binding groups required for the proper fit of the glycolytic intermediates to the active sites of their corresponding enzymes.

Apart from ATP, there are other compounds of high energy transfer whose make up includes phosphate. Creatine phosphate is a storage form of energy in muscles and other excitable tissues such as brain and nerve tissues (Lehninger, 1984). It functions to keep the ATP concentration in these tissues at constant high levels for their normal fraction. Nicotinamide adenine dinucleotide (NAD) and nicotinamide adenine dinucleotide phosphate (NADP) which are coenzymes derived from nicotinic acid and promote oxidation-reduction reactions in biological processes are also made up of phosphate (Lehninger, 1984). Thiamin pyrophosphate which is a coenzyme form of thiamine and serves as an intermediate carrier of aldehyde group to an acceptor molecule (eg. the reaction catalyzed by pyruvate decarboxylase) is yet another example. Thus, P plays an important role in energy transfer in cells and activation of several B-vitamins by phosphorylation.

The most abundant membrane lipids, phospholipids contain phosphorus in the form of phosphoric acid groups. Of these phospholipids, phosphatidylcholine is the most common (Lehninger, 1984). These phospholipids serve primarily as structural elements of membranes and nerves and influence cell permeability (Underwood, 1981; Lehninger, 1984).

Phosphorus is required by bacteria for cellulose digestion and for synthesis of microbial protein (Underwood, 1981). Durand and Kawashima (1980) estimate the requirement level of rumen microbes for P as 3.7 to 4 g/kg digestible organic matter. Cohen (1975) indicated that the presence of water soluble phosphate in the ruminal ingesta was essential for the maintenance of normal flora; thus, it may be necessary to supplement P deficient diets with water soluble phosphates to maintain satisfactory ruminal digestion (Cohen, 1975). Many workers have reported osteomalacia, bone fractures, swollen joints and stiffened gait in cattle which graze pastures of low P content, indicating that P is essential for the rigidity of bone.

Homeostasis

In ruminants the daily urinary excretion of phosphate is generally much less than in nonruminants of similar size (Barlet and Care, 1972), but it can be increased by administration of parathyroid hormone (Mayer et al., 1966; Barlet and Care, 1972). The ruminant recycles more P through saliva than non-ruminants (Church, 1988). This contributes to total P homeostasis (Church, 1988). Bovine saliva contains about 100 mg P per deciliter (Church, 1988). This is about l6 times the level of P in plasma (Church, 1988). Parathyroid hormone stimulates secretion of P in saliva (Church, 1988).

Animals fed diets low in P adapt via a humeral mechanism so that the efficiency of the process by which P is absorbed from the small intestine is increased (Fox and Care, 1978). The common mechanism for the adaptive change to a diet low in either P or Ca is thought to involve an increased production of 1,25 $(OH)_2D$ in the kidney from circulating 25-hydroxycholecalciferol (Kenny, 1982). Mayer et al. (1967) reported that PTH decreases excretion of P in cows while Fox and Care (1978) demonstrated that PTH also increases P absorption, an effect which is considered to be mediated via stimulated production of $1,25(OH)_2D$.

Absorption

Phosphorus occurs in the plant principally as inorganic P (Butler and Jones, 1973). Phytate occurs in seeds but not in vegetative material, and while P in this form is relatively unavailable to non-ruminant species (Little, 1982), ruminants are able to utilize it quite efficiently, because phytate is readily broken down in the rumen by microbial activity (Church, 1988). The detrimental effects of phytate on the absorption of Ca, Zn and other mineral elements are much less in ruminants because the phytate is degraded (Church, 1988). Phosphorus absorption is about 90% efficient in young calves and 55% in cows (Church, 1988).

Absorption of P from the reticulo-rumen is negligible (Little, 1982) and it has not been clearly demonstrated that P is absorbed from the abomasum. Some P absorption occurs in the omasum (Little, 1982). However, the main site of P absorption is the small intestine and its transport consists of both active and passive diffusion (Church, 1988; Arnaud and Sanchez, 1990). Passive diffusion predominates at high luminal concentrations of P (Cohen, 1975). Thus, in P deficiency, P absorption will have a higher energy cost. Active diffusion of P across the small intestine is independent of Ca transport and is achieved by a different path (Cohen, 1975). There is only a small absorption of P from the large intestine. Absorption of P in the small intestine is increased by vitamin D_3 which may either change membrane permeability, alter the configuration of a P carrier, or stimulate production of pump sites (Church, 1988). Excessive magnesium does not appear to affect utilization of P in sheep (Cohen, 1975) and Standish et al. (1971) found no adverse effect of high iron diets on P absorption in steers. In feeding forages with high nitrogen, Stillings et al. (1964) obtained improvement of P retention in Merino wether sheep. Mudgal and Ray (1969) suggested that a reduction in the amount of protein in the diet may result in reduced P retention in calves. However, Little (1968) obtained a marked increase in feed intake and liveweight gain with the addition of P to Stylosanthes humilis when fed to beef cattle. These results suggest that the response to P supplements may be closely associated with the amount of sulphur and the amount and form of nitrogen in the diet.

Leibholz (1974) reported decreased digestibility of P was reduced in sheep given low energy diets, thus suggesting that adequate energy in the diet is needed for the absorption of P. Similarly, McMeniman and Little (1974) obtained a response to P supplements given to sheep only in the presence of a molasses supplement.

Hartmanns (1971) reported significant increases in apparent absorption and retention of P following provision of a calcium supplement which changed the Ca:P ratio from 1.2 to 2.7 in cattle. In that study, the dietary P level was more than adequate at .41% and it has been suggested by ARC (1980) that a wide ratio is deleterious when the diet is deficient in P. This combination occurs frequently in the tropics (Little, 1970), but under these circumstances the extent to which the response to a P supplement is due to the correction of an inappropriate ratio rather than the direct correction of deficiency is open to debate (Little, 1982).

Requirements

Because many forages contain inadequate levels of P to meet the requirements of growing or lactating cattle (McDowell et al., 1983) and because P deficient soils are common, P deficiencies in cattle are widespread. Dietary P requirements as a percentage of ration dry matter is .19 to .25% for beef cattle (Church, 1988).

Magnesium

Introduction

Magnesium (Mg) is widely distributed among plant and animal tissues, with about 70% of body Mg occurring in the bone (Underwood, 1981). As a soft tissue cation, Mg ranks second to potassium in quantity (Altura et al., 1985). Soft tissues contain .1 to .2 g mg per kg (ARC, 1980). It is associated predominantly with the mitochondria (Underwood, 1981). Only 1% of Mg occurs in the extracellular fluid (Minson, 1990).

Magnesium is an essential element in the diet of animals (Underwood, 1981). Problems associated with the availability of Mg from pasture impose special difficulty at certain strategic times of the year. Cattle turned out to spring pasture suffer a sudden change in diet, from that of concentrates and conserved forage to fresh grass which may have been fertilized with nitrogen and potassium, both of which inhibit absorption of Mg (Payne and Payne, 1987). Spring and winter pastures generally have low Mg levels (Payne and Payne, 1987). Because of fertilization of pastures with potassium in summer, such pastures are more likely to be Mg deficient during late summer and early fall.

Physiological Functions

Studies in molecular biology have established that interrelations exist among the three major biologic macromolecules: DNA, RNA and proteins (Aikawa, 1981). Genetic information stored in DNA is transcribed into mRNA which in turn translates that information into amino acid sequences in the newly synthesized protein (Aikawa, 1981). In each of these processes, Mg plays a vital role.

Protein synthesis and growth

Magnesium activates the enzymes that are involved in nucleotide synthesis (White et al., 1968). For example, nucleoside diphosphokinase catalyzes the reaction that converts ribo and deoxyribonucleotide diphosphates to the triphosphates (White et al., 1968). The ribonucleoside triphosphates are utilized in the formation of all types of RNA and DNA (Miller et al., 1965; White et al., 1968; Darnell et al., 1990). Whitefield et al. (1969) reported increased mitogenic action with increased concentration of Mg in rat thymic lymphocytes indicating that Mg stimulates the initiation of DNA synthesis. The physical size of RNA is controlled by the concentration of Mg (Aikawa, 1981).

The activation, initiation, and elongation stages in protein synthesis need Mg for these processes to take place. The activation stage takes place in the cytosol. In this stage, each of the 20 amino acids are covalently attached to a specific tRNA and the reactions are catalyzed by aminoacyl-tRNA synthetase which is Mg dependent (Lehninger, 1984). The same enzyme (aminoacyl-tRNA synthetase) which is activated by Mg is used in the initiation stage (Lewin, 1970; Lehninger, 1984).

The principal function of the ribosome is synthesis of protein (Aikawa, 1981). The rate of protein synthesis is proportional to the number of ribosomes present (Aikawa, 1981). The only cell devoid of ribosomes is the adult erythrocytes (Aikawa, 1981). The physical size of the RNA aggregates is controlled by the concentration of Mg, and polypeptide formation cannot proceed unless Mg concentration is optimal (Aikawa, 1981).

Other Functions

Magnesium serves as an activator of many enzymes (McDowell et al., 1983). The most important among these are those that hydrolyze and transfer phosphate groups, including the enzymes concerned with reactions involving ATP. For example, in glycolysis, formation of glucose-6-phosphate from glucose require ATP and Mg for phosphorylation to take place. The reaction is catalyzed by hexokinase (Neely and Morgan, 1974; Lehninger, 1984). In the formation of fructose 1-6-diphosphate (fructose-6-phosphate + ATP + Mg) = (ADP + Fructose 1-6-diphosphate) from fructose-6-phosphate, the reaction is catalyzed by phosphofructokinase which needs Mg for phosphorylation (Neely and Morgan, 1974; Lehninger, 1984). The second phase of glycolysis which is concerned with energy conservation also involves Mg in some critical stages. This occurs in four stages (Lehninger, 1984): 1) conversion of 3-phosphoglycerol phosphate to 3-phosphoglycerate (3-phosphoglycerol phosphate + ADP + Mg = 3-phosphoglycerate + ATP) is catalyzed by phosphoglycerate kinase which needs Mg for its action, 2) 3-phosphoglycerate is catalyzed by phosphoglycerate mutase which is activated by Mg to yield 2-phosphoglycerate, 3) 2-phosphoglycerate is catalyzed by enolase that is activated by K and Mg to yield phosphoenolpyruvate (PEP), and 4) the enzyme, pyruvate kinase (PEP + ADP + Mg + Pyruvate) is activated by Mg to convert PEP to pyruvate.

Magnesium activates the enzymes that are involved in the formation of coenzyme nucleotides (White et al., 1968). For example, flavokinase requires

Mg to form flavin mononucleotide with riboflavin and ATP. Flavin nucleotide pyrophosphorylase requires Mg to form flavin adenine dinucleotide from flavin mononucleotide and ATP. Synthesis of pyridine nucleotides also requires Mg. The reaction is catalyzed by the enzyme, diphosphopyridine nucleotidepyrophosphorylase which is activated by Mg (White et al., 1968). Among the other enzymes that are activated by Mg is alkaline phosphatase which is necessary in the formation and maintenance of bone. Diphosphopyridine nucleotide phosphorylase is also dependent on Mg for its activity (Aikawa, 1981).

Along with ATP, Mg is also required for glucose utilization, fat synthesis, muscle contraction and methyl group transfer other than for protein, nucleic acid and coenzyme synthesis (Aikawa, 1981). Thus, interference with Mg metabolism can affect all these functions.

Homeostasis

No single evidence indicates that any single hormone or vitamin is concerned principally and directly with Mg homeostasis. There is evidence that alterations in dietary or blood Ca, total inorganic P, potassium, some of the vitamin D metabolites, PTH, CT and aldosterone can influence Mg homeostasis. Conversely, changes in Mg homeostasis can influence secretion or metabolism of most of these factors. The factors that affect Mg homeostasis are discussed in more detail below.

Calcium. The metabolism of Ca and Mg are closely interrelated. Induced Mg deficiency is associated with hypocalcemia in cattle (Smith, 1961).

Cows and other species that develop hypomagnesemia and concomitant acute hypocalcemia, when fed a Mg-deficient diet, have difficulty obtaining adequate Ca from bone and gut. The animal's ability to mobilize Ca from bone reserves is most evident under conditions in which a sudden substantial Ca demand is placed on these reserves, such as parturition, during heavy lactation, periods of rapid growth, or consumption of a low Ca diet (Littledike and Goff, 1985). In contrast, normal animals consuming a Mg-adequate diet readily adapt to these Ca demand under most conditions. Apparently animals that develop acute Mg deficiency rely mainly upon Ca to sustain normal blood Mg concentrations; if dietary sources are not adequate to needs, hypocalcemia becomes evident (Littledike and Goff, 1985).

Phosphorus. Availability of dietary P can be influenced by dietary Ca, Al, Fe and Mg concentrations (Littledike and Goff, 1985). These minerals form insoluble complexes with dietary P and reduce its resorption. Passive absorption of P is proportioned to dietary P levels; however, active transport of P (Wasserman and Taylor, 1976; Care et al., 1980). Changes in both plasma Ca or P can stimulate 1,25-$(OH)_2D$ production. The 1,25-$(OH_2)D$ can in turn alter Mg homeostasis.

Hormones. Magnesium homeostasis has not been shown to be regulated under normal conditions by a specific hormone. Parathyroidectomy may cause hypomagnesemia (Rayssiguir, 1977) and, conversely, Mg deficiency has been associated with hypoparathyroidism and hypocalcemia which are reversible with Mg repletion (Wacker and Parisi, 1968). Anast et al. (1975) reported that there may be impaired release of PTH and responsiveness to PTH under hypomagnesemic conditions. In vivo studies indicate that hypermagnesemia decreases PTH secretion, while hypomagnesemia increases PTH secretion (Buckle et al., 1968).

Lactation. The occurrence of major hypomagnesemia and hypocalcemia diseases (e.g., milk fever) of cattle is commonly associated with the Mg and Ca demands of lactation. Littledike (1976) reported that in Jersey cattle, initiation of milking was associated with hypocalcemia, hypermagnesemia and hypophosphatemia.

Absorption

Magnesium is absorbed in the rumen, omasum, small intestine, and colon (Tomas and Potter, 1976). This absorption is mediated by an active transport mechanism (Martems and Harmeyer, 1978) especially during low Mg intake (Church, 1988). The passive mechanism is adopted during periods of high or excessive Mg intake (Church, 1988).

Fontenot et al. (1973) reported that high dietary nitrogen did not interfere with Mg absorption. Reid and Jung (1974) on the other hand applied fertilizer nitrogen and increased plant nitrogen from 2% to over 3% and obtained marked reduction in both apparent absorption and retention of Mg. Kemp et al. (1966) related this association of high plant nitrogen and Mg absorption and plasma concentration to the greater production of fatty acids at higher nitrogen levels in the rumen, leading to the possible formation of insoluble Mg soaps and consequently reduced absorption. McGregor and Armstrong (1979) fed a high potassium diet to sheep and obtained reduced Mg absorption from 44 to 20%. Fitt and Hutton (1974) postulated that the deleterious effect of potassium on Mg utilization may operate in part via stimulated microbial activity in the rumen providing increased potential for the binding of Mg to bacterial cell walls (Fitt et al., 1972). Any conditions that result in elevated concentrations of ammonia will in turn increase pH which depresses Mg absorption (Underwood, 1981).

Requirements

The minimum needs of cattle for growth can generally be met by pastures or rations containing 700 ppm Mg (dry basis) (NRC, 1984). The quantity of Mg required in the diet depends on the absolute requirements of the animal and the efficiency of absorption of Mg for the digestive tract (Minson, 1990). Dietary Mg requirement as a percent of ration dry matter is .05 to .25% for beef cattle (Church, 1988). For young calves, the requirement is 12 to 30 mg per kg body weight (NRC, 1984). Daily intake of 20 g Mg is needed to assure the lactating cow does not develop grass tetany (Church, 1988).

Magnesium is also required by rumen microorganisms. Most Mg is located intracellularly in bacteria and microbial requirements are met when animals are fed feeds in which the Mg level exceeds .8 g per kg dry matter (Durand and Kawashima, 1980).

Potassium

Introduction

Potassium (K) is the third most abundant mineral element in the body (NRC, 1984). The predominant cations of the intracellular fluid are K and Mg (Selkurt, 1984). Half to two-thirds of K deficit in the cells is made up by diffusion of sodium into the cells; which is also accompanied by an increase in the cellular concentration of free basic amino acids to maintain cation balance (Leibholz et al., 1966). The predominant anions in the cell are phosphates, sulfates and proteins (Selkurt, 1984). Potassium is also a constituent of extracellular fluid (NRC, 1984). Red blood cells contain approximately 25 times as much K as is present in plasma (NRC, 1984). Muscle and nerve cells are also high in K, containing over 20 times that present in interstitial fluids (NRC, 1984).

Physiological Functions

Protein synthesis and growth

In the elongation stage of protein biosynthesis, the 20 different amino acids are esterified to their corresponding transfer RNAs by 20 different aminoacyl-tRNA synthetase enzymes, each of which is specific for one amino acid and a corresponding tRNA. The elongation process that results into aminoacyl-tRNA compound requires K and Mg (Lewin, 1970). Increased serum K causes release of insulin (Church, 1988) which is a growth factor for cells (Darnell et al., 1990). Insulin stimulates the initiation of peptide-chain synthesis, reflected in an increased ability of ribosomes to translate mRNA. Insulin also accelerates RNA and DNA synthesis, which leads to cell proliferation (Smith et al., 1983).

Severe protein deficiency may be associated with low K. Leibholz et al. (1966) observed low K plasma values in humans with kwashiorkor. Patience et al. (1987) reported that the growth of young pigs fed lysine deficient diets responded to sodium or potassium bicarbonate. Austic et al. (1983) confirmed these results. Lindeman and Pederson (1983) reported an influence of dietary K on the process of protein repletion showing the essential nature of this intracellular cation in reconstruction of tissue protein. Protein depleted rats repleted with adequate calories, vitamins, amino acids, and salts rapidly regained lost weight in the same study. When K was removed from the salt solution, the rats did not regain lost weight, but addition of K allowed protein repletion to resume (Lindeman and Pederson, 1983).

Other Functions

In glycolysis, the fructose 6-phosphate is phosphorylated by ATP in the presence of Mg to form fructose 1, 6-diphosphate (Fructose 6-phosphate + ATP + Mg) = (fructose 1, 6-diphosphate + ADP). This reaction is catalyzed by phosphofructokinase that requires K for its action (White et al., 1973). The transfer of the phosphate of phosphoenolpyruvate to ADP is catalyzed by pyruvate kinase. The resultant product is enolpyruvic acid and ATP. The enzyme has requirement for Mg and functions only in the presence of high K (White et al., 1973).

Amino acids enter cells by an active energy requiring process which occurs against a concentration gradient. Entry of amino acids is accompanied by accumulation of water and some Na and K may leave the cell simultaneously, especially when lysine or arginine enters: thus preserving electrical neutrality of the cell (White et al., 1973).

Together with Mg, potassium is involved in activation of glutamylcysteine synthetase enzyme that catalyses the synthesis of glutamylcysteine from L-Glutamic acid. This compound is a first step in the synthesis of glutathione (White et al., 1973) in amino acid metabolism. The Na, K ATPase mechanism activates the transport of glucose from cells (White et al., 1973). The concomitant K influx and Na efflux in the Na, K ATPase activity is coupled by iodide transport (White et al., 1973). The oxidation of fatty acids in mitochondria to form fatty acyl coenzyme A requires activation of the enzyme acyl CoA synthetase by Mg and K (White et al., 1973).

Potassium is also required by the rumen microorganisms. In growing Aerobacter aerogenes, K has been shown to be associated with the ribosomes and therefore protein synthesis (Durand and Kawashima, 1980). Most rumen bacteria contain enzymes in which their activities require K (Caldwell et al., 1973). Potassium stimulates digestion of cellulose by the micro-organisms. Durand and Kawashima, 1980) observed that K could stimulate in vitro cellulolysis up to 2 g/l. The same authors also observed that rumen microorganisms stimulate synthesis of vitamin B_{12}.

Homeostasis

The secretion of several hormones is regulated by the serum K. Elevated serum K inhibits renin secretion but stimulates synthesis of aldosterone (Smith et al., 1983). The major synthetic pathway for aldosterone is via deoxycorticosterone and corticosterone, which are derived from progesterone by sequential 21- and 11β-hydroxylation (Smith et al., 1983). Corticosterone is converted to 18-hydroxycorticosterone by a mitochondrial 18-hydroxylase. Aldosterone is then produced by the action of the mitochondrial enzyme 18-hydroxysteroid dehydrogenase, which converts the 18-CH_2OH to an aldehyde (Smith et al., 1983).

Aldosterone facilitates the clearance of K from the extracellular fluid, and also K acts as an important stimulator of aldosterone secretion (Berne and Levy, 1988). Conversely, K depletion lowers aldosterone secretion (Berne and Levy, 1988). Several steps in aldosterone biosynthesis are enhanced by K (Berne and Levy, 1988). Aldosterone also lowers serum K by promoting renal excretion of K (Smith et al., 1983).

The enzyme renin that is produced by the kidney, splits a polypeptide, angiotensin 1, from angiotensinogen, a serum α_2-globulin formed by the liver (White et al., 1978). The enzyme, angiotensinase acts on angiotensin 1 to produce angiotensin 11 (White et al., 1978) which in turn acts on the zona glomerulosa to increase aldosterone secretion. The increased aldosterone levels result in Na conservation and K excretion (White et al., 1978).

Absorption

The main absorption site for K is the small intestine (Church, 1988). Potassium is passively absorbed in the jejunum of the small intestine when concentration rises due to absorption of water. It is also passively absorbed in the ileum (Berne and Levy, 1988).

Requirements

Potassium requirement of finishing steers is between .5 and .6% while that of pregnant beef cows is between .5 and .7% (NRC, 1984). Potassium is the mineral present in highest concentration in milk: .15% K compared to .11% Ca and .08% P (Beede et al., 1983). Thus, lactating cows should have a higher requirement for K. The requirement for lactating dairy cows is between .8 and 1.0% (Underwood, 1981). The requirement for K increases under stress, e.g. heat due to increased loss of endogenous K (through sweating and decreased intake due to heat stress) (Beede et al., 1983). Beef cattle also require higher dietary K levels during winter because plants are mature at this time (McDowell et al., 1983). Potassium requirements also vary with the amounts of protein, P, Ca and Na consumed (NRC, 1984).

Sodium

Introduction

Sodium (Na) is the principal cation of the extracellular fluid (Luft, 1990). Body fluids contain about 3.5 g Na per kg (NRC, 1980). In the blood, Na makes up over 90% of the bases of serum but is not present in the blood cells (Underwood, 1981). Na is most likely to be deficient when ruminants receive no mineral supplementation because most forages and grains are deficient in it (McDowell et al., 1983).

Animals crave for salt (NaCl), thus self-feeding of Na sources to correct a dietary deficiency is effective (Church, 1988). Intakes of other elements are regulated by mixing with salt and allowing the Na to determine intake (Church, 1988).

Physiological Functions

Protein synthesis and growth

Increased intracellular Na stimulates Na, K-ATPase (Lingrel et al., 1990). The elevated enzyme activity restores the original transmembrane ionic gradient, thereby maintaining cellular homeostasis (Lingrel et al., 1990). Thyroid hormone, T3 stimulates Na, K-ATPase activity. Elevation of Na, K-ATPase activity is one of the initiating events associated with stretch-induced protein synthesis in embryonic skeletal muscles (Vandenburgh and Kafman, 1981). In cultured fibroblasts, lymphocytes and neuroblastoma cells, activation of Na, K-ATPase is an early and essential step in DNA synthesis and cell proliferation in response to mitogenic stimulation (Kaplan, 1978; Rozengurt and Mendoza, 1980; Mummery et al., 1981).

Other Functions

Sodium functions in maintaining osmotic pressure and body fluid balance (Underwood, 1981; McDowell et al., 1983). In ruminants, Na carries out an essential function in preserving the acid-base balance in the rumen (Minson, 1990). This is important because rumen fermentation yields a variety of acid compounds needing neutralization by sodium bicarbonate secreted in the saliva (Payne and Payne, 1987). This cation is also involved in nerve transmission and active transport of amino acids (Underwood, 1981). It is required for cellular uptake of glucose through activation of the glucose carrier protein.

Homeostasis

Of essential importance for the maintenance of body fluid homeostasis in mammals is that the amount of body water and Na concentration of the extracellular fluid (ECF) are kept within a narrow range (Olsson and McKinley, 1980). Sodium depletion, accompanied by reduced ECF volume activates the renin-angiotensin system and induces hypersecretion of Na-retaining aldosterone from the adrenal cortex (Olsson and McKinley, 1980; Luft, 1990). In addition, Na-depletion (Particularly in herbivorous animals) gives rise to specific appetite which provides a strong motivation to seek and ingest salt (Olsson and McKinley, 1980; McDowell et al., 1983). Excessive intake of Na, on the other hand, primarily elevates the extracellular Na concentration, which induces increased water intake and expansion of the ECF. Consequently, aldosterone secretion is inhibited (Olsson and McKinley, 1980). Antidiuretic hormone (ADH) is mediated by angiotensin 11 when there is depletion of Na (Severs and Severs, 1973) which increases the water permeability of the collecting ducts of the kidney, the end of which is reabsorption and conservation of urinary water (Eckert et al., 1988). The PTH exerts a regulatory effect on proximal tubular anion transport by inhibiting phosphate and bicarbonate reabsorption. As a result, PTH secondarily inhibits proximal tubular Na reabsorption through a mechanism not yet established (Gardenswartz and Schrier, 1982). There is speculation that this proximal tubular inhibition is mediated through the adenylate cyclase system since cyclic AMP results in inhibition of Na and phosphate reabsorption by the proximal tubule (Gardenswartz and Schrier, 1982). Estrogen produces a modest Na retaining effect (Gardenwartz and Schrier, 1982). Gardenwartz and Schrier (1982) have also reported that estrogen increases hepatic angiotensinogen production, thus, increasing plasma renin activity.

Absorption

Transfer of Na and water occurs across the rumen wall into the lumen of the rumen in response to osmotic pressure of the rumen fluid (Church, 1988). Sodium has a net secretion in the small intestine and is nearly completely reabsorbed from the colon in cattle (Church, 1988). The transport of Na across the intestinal epithelium appears to depend on pumps and passive leaks in the cell membrane.

Requirements

The Na requirements of beef cattle have been investigated in a wide range of conditions, in tropical and temperate climates, on good and heavily fertilized pastures and poor natural grazing and at low and high rates of growth and of milk production. Morris and Murphy (1972) reported that reasonable weight gains and feed intakes are realized in beef calves at dietary Na content of .06 to .10%. The NRC (1984) recommends the same values to all classes of beef cattle. Cow's milk averages about .5 g Na per liter. Underwood (1981) reported that .15% Na in the dry diet meets the Na requirements of lactating cows while McDowell et al. (1983) and Church (1988) recommend .18%.

CHAPTER THREE
ADDITIVE AND NONADDITIVE GENETIC EFFECTS OF SERUM CALCIUM, PHOSPHORUS AND MAGNESIUM AND WEIGHT AT WEANING IN AN ANGUS-BRAHMAN MULTIBREED HERD

Introduction

The Angus (A) and Brahman (B) breeds are used extensively in the southern region of the United States in crossbreeding programs for beef production. To meet their nutritional requirements for growth and development, macrominerals including calcium, phosphorus and magnesium are recommended in beef cattle feeding programs. Calcium (Ca) and phosphorus (P) participate in bone formation and magnesium (Mg) is an activator of many enzymes involved in protein and carbohydrate metabolism (McDowell et al., 1983; Littledike and Goff, 1987; Arnaud and Sanchez, 1990; Shils, 1990).

Despite the major role that Ca, P and Mg play in growth and development of beef animals, there are no quantitative genetic studies linking amounts of macrominerals to growth traits. Mineral concentrations in serum have been widely used in nutritional studies to depict the mineral status of animals (Giduck and Fontenot, 1987; Salih et al., 1989; Reffett-Stabel et al., 1989; Orr et al., 1990). Physiologically it is the amount of a macromineral that would be absorbed or excreted to maintain homeostasis with the remainder used for maintenance and production in the metabolic process in the animal. Thus, it seems reasonable to suppose that it is the amount of a mineral in the serum rather than its concentration that may be related to an animal's need for it. In addition, amounts of macrominerals in the serum will explain the growth of the animal better than concentration because accumulation of macrominerals in the animal body (eg. in soft tissues and bone) is a part of the growth and development process. This suggests that amount of macrominerals and growth might, in part, be affected by the same genes. Furthermore, this property of being cumulative makes amounts of macrominerals at a given age suitable for consideration as concomitant traits in multiple trait animal evaluation procedures. Thus, the macromineral traits considered in this study are amounts of Ca, P and Mg in serum.

The objectives of this research were: 1) to estimate differences between A and B breed additive direct and maternal genetic effects for serum Ca, P, Mg and weight at weaning, 2) to estimate A × B nonadditive direct and maternal genetic effects for serum Ca, P, Mg and weight at weaning, and 3) to evaluate the combining ability of straightbred (A and B) and crossbred (.75A .25B, .5A .5B and .25A .75B) sire groups for serum Ca, P, Mg and weight at weaning, when mated across dam breed groups of the same types.

Materials and Methods

Animals

Macromineral and weight records were obtained on 380 calves from a multibreed research herd formed by A, B, and several A × B crosses, in 1989 and 1990. The herd was located at the Pine Acres Research Station of the University of Florida, which is located near Citra. Six sire breed groups consisting of A, .75A .25B, .5A .5B, .25A .75B, B and Brangus (.625A .375B) were mated across five dam breed groups of the same genetic composition as sire groups (except for .25A .75B that were unavailable). The distribution of the number of sires and dams with progeny by breed composition is shown in Table 1. There were a total of 28 sires in the data set. The number of sires per breed group per year ranged from 2 for .75A .25B in 1989 to 5 for Brangus in 1990. Between 1 (for .5A .5B) and 3 (for A and .25A.75B) sires per breed group were represented in both 1989 and 1990. This ensured connectedness in the data set. The number of dams in the data set was 243. There was a minimum of 14 dams (.75A .25B in 1990) and a maximum of 65 dams (A in 1989) per breed group per year. The number of calves produced in 1989 and 1990 by mating subclass (Table 2) ranged from three (.5A .5B sires mated to .75A .25B dams) to 40 (B sires mated to B dams).

Cow management

During most of the year, cows were managed in two separate herds: A and A × B cows in one herd and B cows in another one. Both herds were maintained on bahiagrass (Paspalum notatum) pastures without supplementation. In winter (mid-December to March), they were assigned to six replicated forage supplementation regimens and one control (13 herds), according to breed group of dam and breed group of sire. Supplementation consisted of bermudagrass (Cynodon dactylon) hay, wilted to various percentages of dry matter and urea. Cows were synchronized with Prostaglandin $F_{2\alpha}$ in March (A and A × B) and April (B), then inseminated artificially twice at most. Subsequently, cows were assigned to six separate herds and left with a clean up bull (one clean up bull per breed group of sire) for 60 days.

Records

Weaning weight and six intermediate weights between birth and weaning at approximately five week intervals were measured on calves. Blood samples were taken concurrently with all these weights. Age at first sampling ranged from one day to 85 days (97% of calves were sampled within 70 days of birth). Age at weaning ranged from 151 to 275 days (91% of the calves were weaned between 210 and 270 days of age). About 10 ml of blood were bled from each animal using vacutainer tubes. Blood samples then were centrifuged at 700 g for 30 min in order to separate the serum from the hematocrit. Serum samples were deproteinized using 10% trichloroacetic acid to one mililitre of serum. This made a filtrate that was a 1 to 10 dilution of the serum sample. Flame absorption spectrophotometry (Perkin Elmer model 306) was used to read Ca and Mg, while P was read by the colorimetry method. Mineral concentrations were read against standard solutions (Fick et al., 1979).

Traits

Four traits were defined: serum calcium at weaning (WCa), serum phosphorus at weaning (WP) and serum magnesium at weaning (WMg) and weaning weight (WW). The macromineral trait curves followed the same pattern as weight curves, subsequently all traits were adjusted to 205 days using the formula recommended by the Beef Improvement Federation (BIF, 1990).

Because blood samples could not be taken at birth, amounts of serum Ca, P and Mg as well as weight in a sample close to birth were substituted for their amounts and weight at birth in the BIF adjustment formulas.

The macromineral amounts and weight closest to 205 days of age were considered to be weaning records. The amounts of minerals used in these BIF-like formulae were computed as the product of the concentration times the estimated serum volume for each calf. Mineral concentrations were determined by chemical analyses. Serum volumes were computed as the product of calf weights times the expected fraction of blood in cattle (.077; Frandson, 1975) times the expected fraction of serum in blood (.6; Jesse, 1979).

TABLE 1. NUMBER OF SIRES AND DAMS BY BREED GROUP COMPOSITION

	Sires				Dams			
Breed Group[1]	Total	1989	1990	1989 & 1990[2]	Total	1989	1990	1989 & 1990[3]
A	5	4	4	3	65	65	42	42
.75A.25B	3	2	3	2	18	18	14	14
.5A.5B	4	2	3	1	38	30	33	25
.25A.75B	4	4	3	3	0	0	0	0
B	5	3	4	2	76	52	59	35
BRANGUS	7	4	5	2	46	25	40	19
Total	28	19	22	13	243	190	188	135

[1] A = Angus, B = Brahman.
[2] Number of sires present in both 1989 and 1990.
[3] Number of dams present in both 1989 and 1990.

TABLE 2. NUMBER OF PROGENY BY MATING TYPE

Breed group of dam[1]	Breed group of sire[1]						
	A	.75A.25B	.5A.5B	.25A.75B	B	BRANGUS	TOTAL
A	26	13	7	17	20	24	107
.75A.25B	6	5	3	6	6	6	32
.5A.5B	12	9	5	9	16	12	63
B	14	18	11	15	40	13	111
BRANGUS	8	6	5	8	11	29	67
TOTAL	66	51	31	55	93	84	380

[1] A = Angus, B = Brahman.

Genetic analysis

Best linear unbiased estimates (BLUE) of A additive (expressed as a deviation of A from B) and A × B nonadditive (expressed as A x B plus B x A minus A x A plus B x B) direct and maternal genetic effects were obtained using the two-step procedure described by Elzo *et al.* (1990).

In the first step, the BLUE of A sire additive, A dam additive, A × B calf nonadditive and A × B dam nonadditive genetic effects were estimated using ordinary least squares procedures. In addition to these four genetic effects, the model used for a calf record included year of birth, winter management (forage and breeding management), age at first sampling after birth, sex, age of dam and sex × age of dam interaction as environmental effects, and residual effects. There were three sexes (bulls, heifers and steers) and six age of dam categories (three, four, five, six, seven and eight or more years of age). Calf age was at first sampling was defined as a discrete variable using an interval of five days of age. There were 17 calf age at sampling categories. All genetic effects were assumed to be fixed. Residual effects were assumed to be random with mean zero, common variance and to be uncorrelated. Except for the interaction between sex of calf and age of dam which was significant for WMg ($P < .01$) and WW ($P < .04$), interactions among environmental effects were nonsignificant and excluded from the final model. Genetic effects were defined as regression coefficients. The A sire and dam additive genetic effects were defined as linear functions of the expected fraction of A alleles in the sire and the dam of a calf, respectively. Similarly, the A × B calf and dam nonadditive genetic effects were assumed to be proportional to the expected fraction of AB intralocus combinations in calves and dams.

In the second step, the BLUE of the A additive and A × B nonadditive direct and maternal genetic effects were computed as linear combinations of the BLUE of the genetic effects from step one, as follows: (i) A additive direct genetic effects = 2(A sire additive genetic effect), (ii) A maternal genetic effects = A dam additive genetic effects - A sire additive genetic effects, (iii) A × B nonadditive direct genetic effects = A × B calf nonadditive genetic effects, and (iv) A × B nonadditive maternal genetic effects = A × B dam nonadditive genetic effects. Residual mean square was used to test the significance of the effects in the model.

In order to study the combining ability of breed of sires mated across breed groups of dams, the BLUE of the total genetic value of calves produced by each mating combination was determined. Total genetic values were computed as linear functions of the expected A sire additive, A dam additive, A × B calf nonadditive and A × B dam nonadditive genetic effects in each mating combination. For instance, when .5A.5B sires are mated to .5A.5B (F_1) dams, the calves produced have an estimated total genetic value of .5 (BLUE of A sire additive genetic effect) + .5 (BLUE of A dam additive genetic effect) + .5 (BLUE of A × B calf nonadditive genetic effect) + 1 (BLUE of A × B dam nonadditive genetic effect). Computations were carried out using the generalized least squares program of Statistical Analysis System (SAS, 1985).

Results and Discussion

Amounts of macrominerals are an integral part of the growth and development process in animals (Littledike and Goff, 1987; Shils, 1990). They have a measurable contribution to increments in weight of growing animals. Thus, there is a biological part-whole relationship between amounts of macrominerals in body tissues (e.g., bone, muscle, serum) and weights of animals. Because weights were used here to predict amounts of macrominerals in serum of calves, environmental and genetic effects for these estimated amounts of macrominerals in serum and weight at weaning would be expected to be more similar than those that would have been obtained between direct measurements of serum macrominerals and weight at weaning. This expected differential increment in the results of these analyses could not be quantified in this study because it was not feasible to measure amounts of macrominerals directly in serum.

Environmental effects

Year and sex of calf were the only environmental effects important ($P < .01$, Table 3) for all traits (WCa, WP, WMg and WW) in the study. The significance of year could be due to seasonal effects within the two years that would affect nutrition whereas the significance of sex as a source of variation in these traits is likely due to the biological phenomenon that males are usually heavier than females at comparable ages. This aspect also might give rise to males having more of these macrominerals relative to females. The effect of age of dam was important for WP and WMg (P <

.01). This effect may have been due largely to differences in milk production between younger (first 2 calvings) and older dams. This concurs with studies done by Rutledge et al. (1971). The interaction between sex by age of dam which represents the manner in which each level of sex interacts with each level of age of dam was important for WMg ($P < .01$) and WW ($P < .04$). This indicates that the effect of sex of calf on WMg and WW was different for the various age of dam groups. This might have been because of the influence of sex on milk production from the dams. Winter management was important only for WCa and WW ($P < .01$, Table 3). Calf age at first sampling (i.e., the sample used for the BIF-like correction to 205 days of age) was not important ($P > .4$) for any trait. This was probably due to the short calving season in this herd, where most calves were born within a span of 40 days.

Of the three macromineral traits, WCa was the one that behaved most similarly to WW. Both WCa and WW were affected by the same environmental effects (year, winter management and sex).

The response of WCa and WW to changes in management (winter management) indicates that they were more sensitive to microenvironmental changes than WP and WMg, that were jointly affected by year, sex and age of dam effects. This may have been due to the larger amounts of Ca needed by calves for their growth and by dams for their milk production than those of P and Mg. Church (1988) reported that Ca, and Mg level in milk is respectively 1.23 and .126 g per kg milk. The level of P in milk is .95 g per kg milk (ARC, 1965). Thus, a change in the supply of Ca through milk would have had a larger impact on WCa than changes in the availability of P and Mg would have had on WP and WMg.

Genetic effects

Angus sire additive genetic effects were small (−4.70 ± 1.25 mg WCa, −3.00 ± 1.10 mg WP, −.87 ± .27 mg WMg and −.38 ± .11 kg WW, Table 4) and significant ($P < .01$, Table 3). Angus dam additive genetic effects were also small and nonsignificant for WCa and WW (1.86 ± 1.28 mg WCa and .14 ± .11 kg WW, Table 3, 4). Angus dam additive genetic effects contain .5A direct plus all the maternal additive genetic effects, thus, it is this linear combination of genetic effects that was significantly different in A and B dams for WP and WMg (Table 3). The additive direct genetic effects were significant. Their BLUE were −9.40 ± 2.50 mg WCa, −6.00 ± 2.20 mg WP, −1.74 ± .54 mg WMg and -.76 ± .22 kg WW. The BLUE for additive maternal genetic effects were 6.56 ± 1.79 mg WCa, −8.82 ± 1.58 mg WP, 1.70 ± .39 mg WMg and .52 ± .16 kg WW. These estimates suggest that calves sired by B had better direct genetic abilities for WCa, WP, WMg, and WW and that B dams have genetic abilities to produce calves that have higher WP, while the A dams have genetic abilities to produce calves that have high WCa, WMg and larger WW. This would indicate that B would be more suitable than A as sire breed to maximize or optimize on WCa, WP, WMg, and WW. The A breed would be suitable as dam breed if WCa, WMg and WW were of interest; while B would be suitable as dam breed for WP.

TABLE 3. F-VALUES AND PROBABILITY LEVELS OF ENVIRONMENTAL AND GENETIC EFFECTS FOR SERUM CALCIUM, PHOSHORUS AND MAGNESIUM AND WEIGHT AT WEANING

		Trait							
		Calcium		Phosphorus		Magnesium		Weight at weaning	
Source[a]	df	F	P>F	F	P>F	F	P>F	F	P>F
Year	1	38.77	.01	14.71	.01	24.72	.01	16.28	.01
Winter management (year)	24	2.07	.01	1.29	.17	1.39	.11	2.56	.01
Clean up herd (year)	10	1.99	.03	1.20	.29	1.47	.15	1.70	.08
Calf age at first sampling	16	.73	.76	.77	.71	1.04	.41	.58	.90
Sex of calf	2	17.03	.01	12.97	.01	13.75	.01	20.63	.01
Age of dam	5	1.34	.25	2.76	.02	2.65	.02	1.93	.09
Sex of calf x age of dam	10	1.21	.28	1.43	.17	2.30	.01	1.92	.04
Angus sire additive[b]	1	14.14	.01	7.39	.01	10.24	.01	12.23	.01
Angus dam additive[b]	1	2.11	.15	108.94	.01	8.91	.01	1.66	.20
A x B direct nonadditive[c]	1	18.09	.01	3.34	.07	19.57	.01	21.38	.01
A x B maternal nonadditive[c]	1	86.90	.01	7.54	.01	67.51	.01	115.88	.01

[a] Residual mean squares were 5.911 mg^2 for weaning calcium, 4.626 mg^2 for weaning phosphorus, .2791 mg^2 for weaning magnesium and .0435 kg^2 for weaning weight; df residual effects = 308

[b] Angus additive genetic effects are expressed as deviations from Brahman

[c] A x B intralocus nonadditive genetic effects are defined as deviations from those of the parental breeds; A = Angus; B = Brahman

TABLE 4. BEST LINEAR UNBIASED ESTIMATES OF ADDITIVE AND NONADDITIVE GENETIC EFFECTS FOR SERUM CALCIUM, PHOSPHORUS AND MAGNESIUM AND WEIGHT AT WEANING

	Trait			
	Calcium	Phosphorus	Magnesium	Weight at weaning
Genetic effect[a]	mg	mg	mg	kg
Angus sire additive[b]	-4.70 ± 1.25**	-3.00 ± 1.10**	-.87 ± .27**	-.38 ± .11**
Angus dam additive[b]	1.86 ± 1.28**	-11.82 ± 1.13**	.83 ± .28**	.14 ± .11
A x B direct nonadditive[c]	213.51 ± 50.20**	81.19 ± 44.41	48.26 ± 10.91**	19.91 ± 4.31**
A x B maternal nonadditive[c]	366.56 ± 39.32**	95.50 ± 34.79**	70.20 ± 8.54**	36.31 ± 3.37**

[a] A = Angus, B = Brahman

[b] Angus additive genetic effects are expressed as deviations from Brahman

[c] A x B intralocus nonadditive genetic effects are defined as deviations from those of the parental breeds

**P <.01

Intralocus A × B interactions for nonadditive direct genetic effects were substantially larger than A additive direct genetic effects. The BLUE respectively for WCa, WP, WMg, and WW were 22.71, 13.53, 27.74 and 26.20 times larger than A direct additive genetic effects (Table 4).

Intralocus A × B interactions for nonadditive maternal genetic effects were even larger than direct nonadditive genetic effects (Table 4). Their BLUE ($P < .01$) were 366.56 ± 39.32 mg for WCa, 95.50 ± 34.79 mg for WP, 70.20 ± 8.54 mg for WMg and 36.31 ± 3.37 kg for WW. These estimates were 1.72, 1.18, 1.45 and 1.82 times larger than those of A x B nonadditive direct genetic effects. Relative to A maternal additive genetic effect, the BLUE for maternal nonadditive genetic effect were 55.88, 10.83, 41.39 and 69.83 times larger for WCa, WP, WMg and WW respectively. In fact, total (direct plus maternal) nonadditive genetic effects (580.07 ± mg, $P < .01$, for WCa, 176.69 ± 53.49 mg, $P < .01$, for WP, 118.46 ± 13.22 mg, $P < .01$, for WMg and 56.22 ± 5.21 kg, $P < .01$, for WW) accounted for 98.88%, 92.26% , 98.59% and 99.08% of the total (additive plus nonadditive direct and maternal) genetic effects for WCa, WP, WMg and WW, respectively. The large A × B nonadditive direct and maternal genetic effects suggest that A and B have substantially different sets of alleles affecting WCa, WP, WMg, and WW and that these alleles, on the average, interact positively, resulting in larger genetic values for these traits in crossbred calves.

The BLUE of the A × B nonadditive direct genetic effect for WW (19.91 ± 4.31 kg, $P < .01$) was between the estimate computed by Peacock *et al.* (1981):

20.7 ± 2.6 kg , P < .01, and that of Wyatt and Franke (1986): 24.2 ± 1.04 kg, P < .01), and was larger than the value computed by Elzo *et al.* (1990): 9.47 ± 8.96 kg. On the other hand, the BLUE of the A × B nonadditive maternal genetic effect for WW (36.31 ± 3.37 kg, P < .01) was larger than those of Peacock *et al.* (1981): 24.3 ± 2.0 kg, P < .01, Wyatt and Franke (1986): 13.0 ± 1.06 kg, P < .01, and Elzo *et al.* (1990): 20.95 ± 3.56, P < .01. Estimates of A × B nonadditive direct and maternal genetic effects for WCa, WP and WMg for comparison were not found in the literature.

The overall ranking of the BLUE of all genetic effects, from largest to smallest, was: A × B nonadditive maternal, A × B nonadditive direct, A (A minus B) additive direct and A (A minus B) additive maternal for WCa, WMg and WW. The rank for WP followed the same trend as the other traits except in additive genetic effects where maternal was more important than direct. Thus, these macrominerals had similar genetic responses as WW, which adds genetic support to the well-known physiological ties between Ca, P, Mg and growth. The A × B crossbred calves and calves from A × B crossbred dams had larger amounts of serum Ca, P and Mg and larger weights at weaning than A or B straightbred calves. Crossbred (A × B) dams may have achieved their advantage over straightbred dams through greater milk production, a higher fraction of solids in milk or both. Care et al. (1980) reported that there is a positive linear relationship between the percentage absorption of Ca and the rate of milk secretion, from which it was determined that 80% of the lactational loss of Ca was compensated by an increase in the efficiency of its absorption. Thus, the crossbred dams might be more efficient than straightbred dams in absorption of Ca and in utilizing Ca for milk synthesis. This might also suggest that crossbred dams have increased production of parathyroid hormone that would in turn result in increased amount of 1,25-dihydroxycholecalciferol to effect increased absorption. Crossbred (A × B) calves may have grown faster than straighbreds because of a larger capacity to consume milk and a better efficiency of utilization of the ingested Ca, P, Mg and other nutrients.

Combining ability of sire breed group and dam breed groups

The combining ability of five breed groups of sires (A, .75A .25B, .5A .5B, .25A .75B, B) and six breed groups of dams (A, .75A .25B, F_1, F_2, .25A .75B, B) is presented in Table 5. Combining ability was expressed as the weighted sum total of additive and nonadditive direct and maternal genetic effects present in each breed group of sire × breed group of dam combination. Because additive genetic effects were expressed as deviations from B and nonadditive genetic effects as deviations from intrabreed interactions, B calves had zeroes for the total genetic values in all traits.

The best combination was given by the mating of B sires to F_1 dams: 474.24 ± 43.64 mg WCa, 130.18 ± 38.61 mg WP, 94.74 ± 9.48 mg WMg and 46.34 ± 3.74 kg WW, all of them significant ($P < .01$). However, these values differ little from those of the mating of F_1 dams to the other breed groups of sires, giving the F_1 dams the best overall combining ability for all breed groups of dams. This was because: 1) F_1 dams express 100% of the A × B nonadditive maternal genetic effects, and these were the largest of all genetic effects, ii) calves from F_1 dams and sires of any AB expected breed composition show 50% of the A × B nonadditive direct genetic effects, and these were the second largest genetic effects, and iii) A minus B additive direct and maternal genetic effects were very small, rendering them almost immaterial to the BLUE of total genetic values.

The second best overall combining ability corresponded to F_2 dams for the same reasons indicated for F_1 dams, except that they were expected to express only 50% of the A × B nonadditive maternal genetic effects.

The worst combination was given by the mating of A sires and A dams: -2.83 ± 1.68 mg WCa, -14.82 ± 1.48 mg WP ($P < .01$), $-.04 \pm .36$ mg WMg and $-.23 \pm .14$ kg WW. Only additive direct and maternal genetic effects were responsible for these differences.

In contrast to dam breed groups, there was no sire breed group that was uniformly better than the rest when mated across dam breed groups. Large differences in A × B nonadditive maternal genetic effects among specific sire group × dam group combinations were the main reason for it, followed closely by differences in A × B nonadditive direct genetic effects.

The ranking of the sire breed group × dam breed group combinations based on total genetic effects was the same for WCa, WP, WMg and WW. This resulted as a consequence of the equal ranking of the additive and nonadditive direct and maternal genetic effects for all these traits.

TABLE 5. COMBINING ABILITY OF SIRE BREED GROUPS MATED ACROSS DAM BREED GROUPS FOR SERUM CALCIUM, PHOSPHORUS AND MAGNESIUM AND WEIGHT AT WEANING

Breed group		Breed group of sire[1]				
of dam[1]	Trait[2]	Angus	.75A.25B	.5A.5B	.25A.75B	Brahman
Angus	WCa	-2.83 ± 1.68	51.72 ± 12.63**	106.27 ± 25.10**	160.82 ± 37.61**	215.37 ± 50.14**
	WP	-14.82 ± 1.48**	6.23 ± 11.17	27.27 ± 22.21	48.32 ± 33.28	69.37 ± 44.35
	WMg	-.04 ± .36	12.24 ± 2.74**	24.53 ± 5.45**	36.81 ± 8.17**	49.09 ± 10.89**
	WW	-.23 ± .14	4.84 ± 1.08**	9.91 ± 2.15**	14.98 ± 3.23**	20.06 ± 4.30**
.75A.25B	WCa	187.54 ± 18.00**	215.40 ± 22.26**	243.26 ± 27.30**	271.12 ± 32.76**	298.98 ± 38.47**
	WP	44.24 ± 15.92**	55.14 ± 19.69**	66.04 ± 24.15**	76.94 ± 28.98**	87.84 ± 34.03**
	WMg	38.14 ± 3.91**	44.39 ± 4.84**	50.64 ± 5.93**	56.89 ± 7.12**	63.14 ± 8.36**
	WW	18.33 ± 1.54**	20.91 ± 1.91**	23.49 ± 2.34**	26.08 ± 2.81**	28.66 ± 3.30**
.5A.5B(F_1)	WCa	469.54 ± 43.64**	470.72 ± 43.64**	471.89 ± 43.64**	473.07 ± 43.64**	474.24 ± 43.64**
	WP	127.18 ± 38.61**	127.93 ± 38.60**	128.68 ± 38.60**	129.43 ± 38.61**	130.18 ± 38.61**
	WMg	93.87 ± 9.48**	94.09 ± 9.48**	94.31 ± 9.48**	94.52 ± 9.48**	94.74 ± 9.48**
	WW	45.96 ± 3.74**	46.06 ± 1.91**	46.15 ± 3.74**	46.25 ± 3.74**	46.34 ± 3.74**
.5A.5B(F_2)	WCa	286.51 ± 29.71**	287.44 ± 29.70**	288.61 ± 29.68**	289.79 ± 29.67**	290.96 ± 29.67**
	WP	79.43 ± 26.29**	80.18 ± 26.27**	80.93 ± 26.26**	81.68 ± 26.25**	82.43 ± 26.24**
	WMg	58.78 ± 6.46**	58.99 ± 6.45**	59.21 ± 6.45**	59.43 ± 6.45**	59.64 ± 6.45**
	WW	27.81 ± 2.55**	27.90 ± 2.55**	28.00 ± 2.55**	28.09 ± 2.55**	28.18 ± 2.55**
.25A.75B	WCa	293.36 ± 38.59**	267.84 ± 32.84**	242.33 ± 27.34**	216.81 ± 22.27**	191.30 ± 18.00**
	WP	90.75 ± 34.14**	81.35 ± 29.05**	71.95 ± 24.18**	62.55 ± 19.70**	53.15 ± 15.92**
	WMg	61.86 ± 8.38**	56.04 ± 7.14**	50.23 ± 5.94**	44.41 ± 4.84**	39.00 ± 3.91**
	WW	28.21 ± 3.31**	25.82 ± 2.82**	23.42 ± 2.35**	21.03 ± 1.91**	18.63 ± 1.54**
Brahman	WCa	208.81 ± 50.31	156.61 ± 37.74**	104.41 ± 25.16**	52.20 ± 12.58**	0
	WP	78.19 ± 44.51	58.64 ± 33.38	39.09 ± 22.25	19.55 ± 11.13	0
	WMg	47.39 ± 10.93**	35.54 ± 8.20**	23.70 ± 5.47**	11.85 ± 2.73**	0
	WW	19.54 ± 4.32**	14.66 ± 3.24**	9.77 ± 2.16**	4.89 ± 1.08**	0

[1] A = Angus, B = Brahman.

[2] Total genetic values for WCa, WP and WMg are expressed in mg, and for WW in kg.

**P < .01

CHAPTER FOUR
HERITABILITIES OF AND GENETIC, ENVIRONMENTAL AND PHENOTYPIC CORRELATIONS AMONG SERUM CALCIUM, PHOSPHORUS AND MAGNESIUM AND WEIGHT AT WEANING IN AN ANGUS-BRAHMAN MULTIBREED HERD

Introduction

Identification and study of components of growth suitable for genetic evaluation of animals in multibreed populations is needed to improve the accuracy of prediction of genetic values for growth traits, especially in small populations. Primary candidates are traits with known biochemical and physiological links to growth, such as macrominerals. Calcium (Ca), phosphorus (P) and magnesium (Mg) are three macrominerals that have essential roles in growth and development. These macrominerals are involved in activation of enzymes for protein synthesis (Ca, P, Mg), bone formation (Ca, P) and, possibly, hypothalamic regulation (Mg) of feed intake (Lewin, 1970; Ammerman *et al.,* 1971; Seoane *et al.*, 1975; Horowitz and Weistein, 1983; Reeds, 1989; Arnaud and Sanchez, 1990; Brostrom and Brostrom, 1990; Darnell *et al.*, 1990).

Beef cattle requirements of Ca, P and Mg for preweaning growth normally are met using a supplement in the form of mineral blocks or licks. The cost of mineral supplementation is higher in subtropical and tropical areas than in temperate zones, rendering mineral supplementation prohibitively expensive in some developing countries (McDowell *et al.*, 1983). Incidence of deficiencies of Ca and P is higher in subtropical and tropical than in temperate regions (McDowell *et al.*, 1983). Deficiencies of Ca, P and Mg not only are clinical but also are subclinical, thus difficult to detect; thus can result in reduced weaning weights (Hardt *et al.*, 1989). Amounts of Ca, P and Mg in serum at weaning are three traits that may aid in the selection of animals for preweaning growth. In order to use these traits to evaluate animals genetically using multiple trait mixed model procedures (Henderson and Quaas, 1976; Quaas and Pollak, 1980), genetic, environmental and phenotypic variances of and covariances among all these traits need to be estimated. Thus, the objectives of this research were: 1) to estimate heritabilities of amounts of serum Ca, serum P, serum Mg and weight at weaning (WCa, WP, WMg and WW), 2) to estimate additive genetic, environmental and phenotypic correlations among WCa, WP, WMg and WW.

Materials and Methods

Records of macrominerals in serum (WCa, WP and WMg) and weight (WW) at weaning from 380 calves produced by the matings of five Angus (A), five Brahman (B), three .75A.25B, four .5A.5B, four .25A.75B and seven Brangus (.625A.375B) sires across 65 A, 76 B, 18 .75A.25B, 38 .5A.5B and 46 Brangus dams were collected in 1989 and 1990, at the Pine Acres Research Station of the University of Florida, Citra. All records were adjusted to 205 days using the Beef Improvement Federation (BIF, 1990) recommendations, with an initial value close to birth substituted for the one at birth in the BIF adjustment formula because blood samples were not collected at birth. All bulls were unrelated except two .5A.5B bulls that were half sibs. Calf age at weaning ranged between 151 and 275 days (91% of the calves were weaned between 210 and 270 days of age). Age at first sampling ranged between one day and 85 days (97% of calves were sampled within 70 days of age).

The macromineral amounts and the weight closest to 205 days were used as weaning records. Amounts of macrominerals were obtained by multiplying estimated serum volume by concentration. Serum volume was computed as the product of the expected fraction of serum in blood (serum volume/blood volume = .6; Jesse, 1979) times the expected fraction of blood in cattle (blood weight/animal weight = .077, Frandson, 1975) times the weight of the animal. Serum concentrations of Ca and Mg were measured by flame absorption spectrophotometry (Perkin Elmer Model 306) of serum samples deproteinized with 10% trichloroacetic acid, whereas the concentration of P was determined by colorimetry (Fick *et al.*, 1979).

To ensure connectedness across years, at least one bull from each breed group was used to sire calves both in 1989 and in 1990. The number of progeny per sire and year fluctuated between two and 34 (Table 6). Artificial insemination (first two cycles after synchronization with Prostaglandin $F_{2\alpha}$) and natural service were used in all breed groups of dams. There was one natural service bull per breed group of sire, resulting in a total of six breeding herds. Natural service bulls were kept with the cows for 60 days. Subsequently, dams were assigned to only two groups: A and all A × B crossbred groups in one herd and B in another (June to mid-December). Both groups of cows were maintained on bahiagrass pastures (Paspalum notatum) with a complete free-choice mineral supplement only (i.e., no supplement of protein or energy). In winter (mid-December to March), dams were allocated into six replicated supplementation regimens consisting of bermudagrass (Cynodon dactylon) hay sun-dried to various dry matter percentages, molasses and urea.

Estimation of Heritabilities and Genetic, Environmental and Phenotypic Correlations

Variance components were estimated using the restricted maximum likelihood (REML) method (Patterson and Thompson, 1971; Corbeil and Searle, 1976). Since all traits were measured in all animals, computations were carried out using the single-trait REML option of the program PROC VARCOMP of the statistical analysis system (SAS, 1985).

The mixed model used contained year, winter management within year, natural service herd within year, age at first sampling after birth, sex of calf, age of dam and sex by age of dam interaction as environmental effects, breed group of sire × breed group of dam interaction, breed group of maternal grandsire × breed group of maternal granddam interaction and sire within breed group of sire as genetic effects, and residual. Environmental and genetic effects were assumed to be fixed. Sires and residuals were assumed to be random, each with mean equal to zero, common variance and uncorrelated. The sire variance represented .25 additive direct genetic variance.

The residual variance contained .75 additive direct genetic variance, additive maternal genetic variance, nonadditive direct and maternal genetic variances, covariances between direct and maternal random genetic effects and variances due to random environmental effects. Variance components (sire, residual) for WCa, WP, WMg and WW were estimated using the same mixed model. Phenotypic variances and covariances were computed as the sum of the sire plus the residual variances.

Heritabilities were computed as four times the estimate of the sire variance divided by the phenotypic variance. Standard errors of heritability estimates were computed as four times the variance of the intraclass correlation among halfsibs [(Falconer, 1981)]. The formula of the variance of the intraclass correlation among halfsibs used was:

$$\sigma_t^2 = 2[1 + (n - 1)t]^2(1 - t)^2 / n(n - 1)(N - 1)$$

where:

σ_t^2 = Sampling variance of the intraclass correlation.

n = Average number of progeny per sire (= 13.57).

N = Number of sires (= 28).

$t = h^2/4$ = Intraclass correlation.

TABLE 6. NUMBER OF PROGENY PER SIRE

Breed group[1]	Sire number	Year 1989	Year 1990	Total
Angus	1	7	10	17
	2	8	5	13
	3	7	3	10
	4	16	0	16
	24	0	10	10
.75A.25B	5	20	18	38
	6	6	2	8
	25	0	5	5
.5A.5B	9	2	4	6
	10	6	0	6
	26	0	13	13
	27	0	6	6
.25A.75B	12	9	0	9
	13	4	1	5
	14	6	4	10
	15	10	21	31
Brahman	16	5	4	9
	17	34	0	34
	18	7	33	40
	19	0	4	4
	29	0	5	5
Brangus	20	11	0	11
	21	21	3	24
	22	7	4	11
	23	5	0	5
	30	0	6	6
	31	0	4	4
	32	0	24	24
Total		191	189	380

[1] A = Angus, B = Brahman.

Because the REML program of PROC VARCOMP is for a single trait only, covariances were estimated using the formula .5 [estimate of variance (trait 1 + trait 2) - estimate of variance (trait 1) - estimate of variance (trait 2)], as suggested by Searle and Rounsaville (1974). Consequently, REML estimates of sire and residual variance components were estimated for the sums of all possible pairs of traits (WCa + WP, WCa + WMg, etc.). Then, additive genetic, environmental and phenotypic covariances were computed for all pairs of traits. Environmental covariances were computed as the difference between the estimate of the residual covariance minus three times the sire covariance. Environmental variances also were computed in the same fashion. Phenotypic covariances were obtained by adding sire covariances to residual covariances. Finally, genetic, environmental and phenotypic correlations among pairs of traits were computed as the ratio of the appropriate covariances to the product of the standard deviations. Standard errors of genetic correlations were computed using the formula suggested by Falconer (1981). The formula used was

$$\sigma_{(g)} = \frac{1 - g^2}{\sqrt{2}} \left[\frac{\sigma(h_x^2)\,\sigma(h_y^2)}{h_x^2\, h_y^2} \right]^{.5}$$

where:

$$g = \frac{cov_{xy}}{(var\ x\ var\ y)^{.5}}$$

x = First trait.

y = Second trait.

σ = Standard error.

Results and Discussion

Estimates of sire and residual variances for all traits (WCa, WP, WMg, WW) and sums of pairs of traits (WCa + WP, WCa + WMg, et cetera) are shown in Table 7 accompanied by the asymptotic standard errors. Estimates of residual variances were consistently estimated with higher accuracy than sire variances.

Heritability estimates were in the medium range (.39 ± .17 WCa, .40 ± .17 WP, .36 ± .16 WMg, .35 ± .16 WW, Table 8). Thus, selection of animals for or against WCa, WP and WMg seems feasible. A possible selection goal could be to choose those animals that achieve large WW with comparatively low requirements of Ca, P and Mg. This selection goal implies that the selected animals make more efficient use of these minerals to reach a given WW than the unselected ones, and that WCa, WP and WMg are genetically correlated to WW. Estimates of genetic correlations between WW and WCa, WP and WMg were high and positive (1.00, .78, .86). Also, all estimates of genetic correlations among macromineral traits were positive (.66 ± .17 for WCa and WP, .70 ± .16 for WCa and WMg, and .50 ± .23 for WP and WMg).

High values of genetic correlations among WCa, WP, WMg and WW were expected because of the known physiological relationships among these traits. The same hormones (parathyroid hormone, 1,25-dihydroxycholecalciferol, calcitonin) regulate their role in growth and development.

TABLE 7. RESTRICTED MAXIMUM LIKELIHOOD ESTIMATES OF VARIANCE COMPONENTS FOR SERUM CALCIUM, PHOSPHORUS AND MAGNESIUM AND WEIGHT AT WEANING

Trait[1]	Variance component estimate[2]	
	Sire	Residual
WCa	5458.18 ± 3620.92	50223.60 ± 4428.62
WP	4663.67 ± 3119.99	41544.15 ± 3670.32
WMg	243.93 ± 178.11	2443.89 ± 216.30
WW	34.76 ± 25.00	363.92 ± 32.11
WCa + WP	16777.54 ± 11055.03	142811.13 ± 12625.60
WCa + WMg	7307.76 ± 4934.03	68287.34 ± 6025.51
WCa + WW	6363.99 ± 4205.89	58035.86 ± 5117.87
WP + WMg	5967.53 ± 4135.90	54276.74 ± 4804.25
WP + WW	5325.12 ± 3532.65	46644.25 ± 4121.07
WMg + WW	437.60 ± 313.42	4204.95 ± 372.28

[1] WCa, WP, WMg, WW = serum Ca, P, Mg and weight at weaning.

[2] Estimates of variance components are expressed in mg^2 for WCa, WP and WMg, in kg^2 for WW, in $(mg + mg)^2$ for sums of macromineral traits and in $(mg + kg)^2$ for sums of macromineral traits and WW.

Parathyroid hormone activates 1,25- dihydroxycholecalciferol (1,25-$(OH)_2D_3$), which in turn causes an increase in the absorption of Ca, P, and possibly Mg, in the intestine. On the other hand, calcitonin increases the excretion of Ca, P and Mg in the urine and(or) decreases their resorption from skeletal tissue (Littledike and Goff, 1987; Arnaud and Sanchez, 1990; Shils, 1990, Hardwick *et al.*, 1991). Estimates of environmental correlations among macromineral and weight traits at weaning, like the estimates computed for genetic correlations, were also positive, ranging from .51 between WP and WMg to .86 between WCa and WW (Table 8). External environmental stimuli may have contributed to create these environmental correlations. For instance, irradiation of the skin with ultraviolet light from the sun causes 7-dehydrocholesterol to become 1,25-$(OH)_2D_3$, which in turn increases the efficiency of intestinal absorption of Ca, P and, perhaps, Mg (Littledike and Goff, 1987; Hardwick *et al.*, 1991).

Estimates of phenotypic correlations (Table 8) fluctuated between .51 (WP, WMg) and .88 (WCa, WW), and generally were lower than the estimates of genetic correlations and larger than the environmental correlations.

No estimates of heritability for WCa, WP, WMg and of genetic environmental and phenotypic correlations among these traits and with WW were found in the literature.

TABLE 8. ESTIMATES OF HERITABILITIES (±SE) AND GENETIC (±SE), ENVIRONMENTAL AND PHENOTYPIC CORRELATIONS AMONG SERUM CALCIUM, PHOSPHORUS AND MAGNESIUM AND WEIGHT AT WEANING[1]

	Trait			
Trait[2]	WCa	WP	WMg	WW
WCa	.39 ± .17	.66 ± .17	.70 ± .16	1.00 ± NE
WP	.55(.57)	.40 ± .17	.50 ± .23	.78 ± .12
WMg	.71(.70)	.51(.51)	.36 ± .16	.86 ± .08
WW	.86(.88)	.60(.63)	.73(.75)	.35 ± .16

[1] Heritabilities on the diagonal; genetic correlations above the diagonal; environmental and phenotypic (in parentheses) correlations below the diagonal.

[2] WCa, WP, WMg, WW = serum Ca, P, Mg and weight at weaning.

NE = Not estimable

The estimate of heritability for WW (.35 ± .16) obtained for this Angus-Brahman multibreed herd was smaller than the value of .44 reported for Angus by Kennedy and Henderson (1975), was equal to the one computed by Nelsen and Kress (1979) also for Angus, and was higher than the estimates of .26 calculated by Malagon and Duran (1985) for Brahman, and of .25 found by Bertrand and Benyshek (1987) for Brangus.

The estimates of heritabilities and genetic environmental and phenotypic correlations were based on measurements taken on animals which had an adequate dietary supply of Ca, P and Mg. However, these genetic parameters may differ substantially under deficiency conditions, especially the correlations. Thus, this research needs to be repeated under various nutritional regimens where the supply of one or more of these macrominerals is insufficient to meet animal requirements. Because this may be unfeasible, identification of animals that require lower amounts of Ca, P and Mg for preweaning growth in a good nutritional environment might, in practice, be the first step for identification of animals capable of adequate growth and development under conditions of limited availability of these minerals. Semen or sires, and dams if feasible, with these characteristics then could be taken to areas with known deficiencies of Ca, P, and(or) Mg, and progeny tested for WCa, WP, WMg and WW under local conditions.

CHAPTER FIVE

ADDITIVE AND NONADDITIVE GENETIC EFFECTS OF SERUM POTASSIUM AND SODIUM AND WEIGHT AT WEANING IN AN ANGUS-BRAHMAN MULTIBREED HERD

Introduction

In the southern region of the U.S., beef cattle, which include the Angus (A) and Brahman (B) breeds and more frequently their crosses, are managed under extensive pasture conditions. The pastures utilized are often low in sodium (Na), especially during summer. In Florida, pastures also are low in K during winter (Kiatoko et al., 1982). In tropical countries, minerals are low for longer periods of time. The lactation period for beef cows in Florida often begins in December and lasts approximately seven months, thus imposing strains on Na and K reserves.

Sodium and K are required for osmotic balance between cells and extracellular fluids and for base regulation and water balance in the animal (Underwood, 1981; Beede et al., 1983). Sodium is largely extracellular and occurs mainly in body fluids and bones whereas K is primarily intracellular and occurs mainly in muscle and nervous tissue (Underwood, 1981). In ruminants, Na preserves the acid base balance in the rumen by neutralizing acidic compounds produced by rumen fermentation (Payne and Payne, 1987).

Because K is predominantly found in muscle, a measurement of total body K usually is used as an index of fat free mass in animals (Gibson, 1990). Potassium is the mineral element present in highest concentration in milk (.15% K compared to .11% Ca, .08% P, .05% Na) (Underwood, 1981; Beede et al., 1983). Thus, K and Na may become limiting factors in high milk producing cows. Since a lactating cow needs a continuous supply of K and has little capacity for body storage for it, she must consume adequate amounts in her diet to meet daily lactation demands (Beede et al., 1983). Potassium activates amino acid chain elongation during protein synthesis (Lewin, 1970). Increased serum K also causes release of insulin (Church, 1988) which is a growth factor for cells (Darnell et al., 1990). Church (1988) reported that, when there is Na deficiency, growth, milk production and body condition are reduced. In both K and Na deficiencies, feed intake also is reduced (Church, 1988). If choices of breed groups are to be made in relation to their potential for use in alternative breeding systems, each breed group needs to be evaluated for additive and nonadditive genetic effects.

From nutritional and physiological standpoints, K and Na seem to influence growth. However, there is little information concerning genetic effects of K and Na and their influence on growth in beef cattle. Thus, the objectives of this study were:

i) To estimate differences between A and B breed additive direct and maternal genetic effects for serum Na and K and weight at weaning;

ii) To estimate A x B nonadditive direct and maternal genetic effects for serum Na, K and weaning weight; and

iii) To evaluate the combining ability of straightbred (A and B breed groups) and crossbred (.75A.25B, .5A.5B (F_1) and .25A.75B) sire breed groups for serum Na and K and weight at weaning when mated across breed groups of dams.

Materials and Methods

Animals

Data were obtained in 1989 and 1990 from calves reared at the Pine Acres Experimental Farm, near Citra, Florida. The calves were from a multibreed herd involving Angus (A), Brahman (B) and intermediate A x B crosses. Six breed groups of sires consisting of A, B, .75A.25B, .5A.5B, .25A.75B and Brangus (.625A.375B) were mated to five dam breed groups of the same genetic composition (except .25A.75B that were unavailable). The distribution of the number of sires used each year is shown in Table 9. A total of 28 sires were used. Thirteen of these were used in both years. This created connectedness in the herd across the two years. The number of dams used in each year are shown in Table 10. There were a total of 243 dams. Of these, 135 dams were used in both years. A total of 380 calves (Table 11) resulted from the mating of breed groups of sire by breed groups of dam. The largest number of calves were from straightbred groups. For example, there were 26 A, 40 B and 29 Brangus calves.

Management

The cows were synchronized for estrus using Prostaglandin $F_{2\alpha}$ and then inseminated artificially. The A and A x B crosses were inseminated in March while B cows were inseminated in April. The cows were then assigned to six clean up herds for 60 days with one clean up bull representing each breed group of sire.

The cows and calves were grazed on bahiagrass (Paspalum notatum) during summer and fall. During winter and early spring (mid-December to March), they were assigned to six replicated, forage supplementation regimens and a control herd. The supplement consisted of molasses and bermudagrass (Cynodon dactylon) hay fortified with urea (32% N). A free choice mineral supplement containing 20% Ca, 9% P, .25% Mg, 6.12% Na and 18.18% Cl was available to the animals throughout the year. Some of the male calves were castrated.

Records

Birth weight, weaning weight (WW) and intermediate weights between birth and weaning were taken at an interval of five to six weeks. Blood samples were taken concurrently with weights except at birth.

TABLE 9. NUMBER OF SIRES USED EACH YEAR BY BREED GROUP

	Number of sires		
Sire breed group[a]	1989	1990[b]	Total[c]
A	4	4 (3)	5
.75A.25B	2	3 (2)	3
.5A.5B	2	3 (1)	4
.25A.75B	4	3 (3)	4
B	3	4 (2)	5
Brangus	4	5 (2)	7
Total	19	22 (13)	28

[a] A = Angus, B = Brahman

[b] Number of sires used in 1990 that were used also in 1989 shown in parenthesis

[c] Total number of different sires used

TABLE 10. NUMBER OF DAMS USED IN EACH YEAR BY BREED GROUP

	Number of dams		
Dam breed group[a]	1989	1990[b]	Total[c]
A	65	42 (42)	65
.75A.25B	18	14 (14)	18
.5A.5B	30	33 (25)	38
B	52	59 (35)	76
Brangus	25	40 (19)	46
Total	190	188 (135)	243

[a] A = Angus, B = Brahman

[b] Number of dams used in 1990 that were also used in 1989 shown in parenthesis

[c] Total number of different dams used

TABLE 11. NUMBER OF CALVES PRODUCED BY BREED GROUP OF SIRE BY BREED GROUP OF DAM SUBCLASS

	Breed group of sire[a]						
Breed group of dam	A	.75A.25B	.5A.5B	.25A.75B	B	BRANGUS	TOTAL
A	26	13	7	17	20	24	107
.75A.25B	6	5	3	6	6	6	32
.5A.5B	12	9	5	9	16	12	63
B	14	18	11	15	40	13	111
BRANGUS	8	6	5	8	11	29	67
TOTAL	66	51	31	55	93	84	380

[a] A = Angus, B = Brahman.

Blood samples were obtained by jugular puncture. Blood samples were then centrifuged at 700 g per 30 min to separate the serum from the hematocrit.

Serum samples were deproteinized using 10% trichloroacetic acid (TCA). The deproteinization process involved adding one milliliter (ml) of serum to 9 ml of TCA. Dilutions of 100 and 1000 were made from the deproteinized samples using deionized water. Concentration of K and Na were read (from the 100 factor dilution for K and 1000 factor dilution for Na) using the flame atomic absorption spectrophotometry method (Fick et al., 1979).

It was assumed that growth is linear from birth to weaning. Swiger et al. (1962) reported that the effect of weaning age on weight at weaning in beef cattle is linear. In a similar study, Marlowe et al. (1965) obtained a linear relationship of growth from birth to weaning in Angus and Hereford calves. The curves for WK and that of WNa followed that of WW closely. Thus, WNa, WK and WW were adjusted to 205 days using the Beef Improvement Federation formula (BIF, 1990). To adjust the K and Na concentration for age at 205 days, the first sample taken after birth was used as a substitute for that at birth. The amount of WK and WNa was calculated as a product of concentration and the approximate serum volume. The serum volume was calculated as the product of weight and the proportion of blood relative to weight of the calf (.077; Frandson, 1975) times the proportion of serum relative to blood in the calf (.6; Jesse, 1979). The amounts of serum WK and WNa were expressed in mg whereas WW was expressed in kg.

Calf age at first sampling after birth was divided arbitrarily into 17 periods of 5 days each (one day through 85 days). Six age groups of dams at calving were represented in the data set (3, 4, 5, 6, 7, and 8 years and above).

Genetic Analysis

Data recorded in the study were classified by year, winter management within year, natural service herd within year, calf age at first sampling after birth, sex, age of dam and the sex by age of dam interaction as fixed environmental effects. Genetic effects were regressions on: Angus sire additive, Angus dam additive, A x B direct nonadditive and A x B dam nonadditive. Genetic effects were assumed fixed. Residual effects were assumed random, distributed with zero mean and having a common variance. Age of dam was tested for quadratic and cubic relationship with WK, WNa and WW but the effects were not significant. Thus, only the linear effect was included in the final model. Similarly, interactions among environmental effects were tested for significance but only the sex x age of dam interaction was found significant and, hence, was included in the final model. The model resulted in a singular matrix because the sum of the proportion of alleles for the additive direct and for the additive maternal components equals one. Subsequently, two restrictions were imposed on the matrix to remove the dependency: 1) A breed additive (direct and maternal) were deviated from B breed and 2) A x B nonadditive genetic effects were deviated from the intrabreed intralocus interaction at one locus.

Best linear unbiased estimates (BLUE) were obtained using the two step procedure described by Elzo et al.(1990). In the first step, the BLUE of A sire additive, A dam additive, A x B direct nonadditive and A x B dam nonadditive genetic effects were estimated using the ordinary least squares procedures. The A sire and dam additive genetic effects were defined as linear functions of the expected fraction of A alleles in the sire and the dam of a calf, respectively. The A x B direct and dam nonadditive genetic effects were assumed to be proportional to the expected fraction of AB intralocus combinations in calves and dams. In the second step, the BLUE of the A additive and A x B nonadditive direct and maternal genetic effects were computed as linear combinations of the BLUE of the genetic effects from step one, as follows: 1) A additive direct genetic effects = 2(A sire additive genetic effect), 2) A maternal genetic effect = A dam additive genetic effects - A sire additive genetic effects, 3) A x B nonadditive direct genetic effect = A x B calf nonadditive genetic effects and 4) A x B nonadditive maternal genetic effects = A x B calf nonadditive genetic effects and 4) A x B nonadditive maternal genetic effects = A x B dam nonadditive genetic effects.

The BLUE of combining ability of breed groups of sires when mated to breed groups of dams was computed as a linear combination of the expected A additive (sire and dam), and nonadditive (direct and dam) genetic effects.

Thus, it was computed as a total of all genetic effects weighted by their corresponding coefficients for the fractions of direct and maternal additive and nonadditive genetic effects.

It was assumed that: 1) all interlocus interactions at two or more loci are negligible, 2) all intralocus interbreed interactions are the same for all interbreed combinations.

Because the subclass numbers were unequal, computations were done using the generalized least squares program of Statistical Analysis System (SAS, 1985).

Results and Discussion

Environmental Effects

Environmental effects for serum WNa and WK and weight at weaning (WW) are shown in Table 12. Only year and sex of calf were important environmental effects common to all three traits ($P<.01$). Church (1988) reported that males have greater percent of body K than females of comparable weight. Thus, the effect of sex might have been significant because males were heavier than females, hence had larger amounts of WK and WNa. Clean up herd was important for WNa ($P<.05$) and WW ($P<.08$). Age of dam was important for WNa ($P<.03$) and WW ($P<.09$). The effect of age of dam may be due to differences in milk yield of younger and older cows. Sex of calf by age of dam interaction was important for WNa ($P < .07$) and WW ($P < .04$). This effect might have been due to the behavioral mechanism that male calves nurse more frequently and as a result their dams produce more milk. This occurred in studies reported by Cundiff et al. (1966) and by Daley et al. (1987).

Winter management within year influenced WNa and WW. This might have been due to the diet the cows were maintained on during the winter. McDowell et al. (1983) reported that winter pastures are deficient in Na. Studies done by Espinoza et al.(1991) showed that beef cattle in central Florida do not get enough Na from forages during winter to meet their nutritional requirements. Thus, it is possible that the cows did not obtain adequate levels of Na to support the milk production on which the calves were dependent. Both WNa and WW were influenced by year ($P<.01$), winter management (year) ($P<.01$) and clean up herd within year ($P<.05$ for WNa, $P<.08$ for WW), thus, suggesting that both traits are similarly affected by the same environmental effects. This also was suggested by the lack of significance for the effect of calf age at initial sampling ($P<.88$ for WNa, $P<.90$ for WW). Thus, WNa followed the pattern of WW better than WK.

TABLE 12. F-VALUES AND PROBABILITY LEVELS OF ENVIRONMENTAL AND GENETIC EFFECTS FOR SERUM POTASSIUM AND SODIUM AND WEIGHT AT WEANING

		Trait					
		Potassium		Sodium		Weight at weaning	
Source[a]	df	F	P>F	F	P>F	F	P>F
Year	1	25.47	.01	11.31	.01	16.28	.01
Winter management (year)	24	1.36	.12	2.13	.01	2.56	.01
Clean up herd (year)	10	.97	.47	1.89	.05	1.70	.08
Calf age at first sampling	16	.81	.67	.61	.88	.58	.90
Sex of calf	2	15.42	.01	14.83	.01	20.63	.01
Age of dam	5	1.66	.14	2.48	.03	1.93	.09
Sex of calf x age of dam	10	1.57	.11	1.76	.07	1.92	.04
Angus sire additive[b]	1	10.16	.01	11.58	.01	12.23	.01
Angus dam additive[b]	1	.04	.83	.52	.47	1.66	.20
A x B direct nonadditive[c]	1	4.35	.04	21.46	.01	21.38	.01
A x B maternal nonadditive[c]	1	23.16	.01	88.26	.01	115.88	.01

[a] Residual mean squares were 50.073 mg^2 for weaning potassium, 3846.212 mg^2 and .0435 kg^2 for weaning weight; df residual effects = 308

[b] Angus additive genetic effects are expressed as deviations from Brahman

[c] A x B intralocus nonadditive genetic effects are defined as deviations from those of the parental breeds; A = Angus; B = Brahman

Genetic Effects

Genetic effects for serum Na and WK and weight at weaning are shown in Table 12. All genetic effects were important for the three traits except the Angus dam additive effect that was not significant (P>.46 for WNa and WK and P<.20 for WW). The BLUE for genetic effects are shown in Table 13. Angus sire additive genetic effect was large, negative and significant (P<.01) for all the traits. The Angus direct additive genetic effect was -216.70 ± 63.68 mg for WNa, -23.16 ± 7.26 mg for K and -.74 ± .22 kg for WW which suggests that B sires had significantly higher genetic abilities for WNa, WK and WW than A sires. Thus, B alleles in sires promoted larger amounts of WNa and WK and higher WW. This agrees with studies done by Bailey (1981) who found B sired calves to exceed (P<.01) progeny of A bulls in WW. Thus, to maximize or optimize these traits, B would be more suitable as a sire breed than A in a crossbreeding program involving A and B breeds.

The A dam additive genetic effects (.5 direct plus maternal) were small and positive with large standard errors for all three traits. Thus, the values (23.44 ± 32.65 mg WNa, .79 ± 3.73 mg WK and .14 ± .11 kg WW) were not significant. This suggests that A and B dams did not differ on these traits. However, A additive maternal genetic effects were large and significant (131.79 ± 56.37 for WNa, 12.37 ± 5.21 for WK, .52 ± .16 for WW; P <.05) indicating that A has better maternal genetic abilities for WNa, WK and WW than B. This would also indicate that the B direct additive genetic effects in the dam was more important than maternal for these traits. However, since the dam effect of A and B breeds were similar, either A or B would be suitable as dams in a crossbreeding program involving A and B breeds to maximize WNa, WK and WW.

Additive genetic effects (sire and dam) accounted for only .9, 1.4 and .9% of the total genetic effects for WNa, WK and WW, respectively. This difference of .5% between WNa and WK and between WK and WW may not be significant. Thus, the proportion of additive genetic effects relative to total genetic effects for WNa, WK and WW was essentially the same for the three traits.

The BLUE for A x B direct nonadditive genetic effects were large, positive and significant for all traits (5931.66 ± 1280.58 mg WNa, 304.58 ± 146.11 mg WK and 19.91 ± 4.31 kg WW). Thus, the interaction of A and B alleles promoted large genetic values for WNa, WK and WW. The A x B non-additive direct genetic effect for WW concurred with 21.20 ± 3.60 kg reported by Peacock et al. (1981) and 24.20 ± 1.04 kg reported by Wyatt and Franke (1986). These results suggest that A x B crossbred calves may be superior to straightbred A and B calves in one or more of grazing efficiency, digestive efficiency, efficiency of absorption of nutrients, metabolism and excretion of Na and K.

TABLE 13. BEST LINEAR UNBIASED ESTIMATES OF ADDITIVE AND NONADDITIVE GENETIC EFFECTS FOR SERUM POTASSIUM, SODIUM AND WEIGHT AT WEANING

	Trait		
	Potassium	Sodium	Weight at weaning
Genetic effect[a]	mg	mg	kg
Angus sire additive[b]	-11.58 ± 3.63**	-108.35 ± 31.84**	-.38 ± .11**
Angus dam additive[b]	.79 ± 3.73	23.44 ± 32.65	.14 ± .11
A x B direct nonadditive[c]	304.58 ± 146.11*	5931.66 ± 1280.58**	19.91 ± 4.31**
A x B maternal nonadditive[c]	550.72 ± 114.44**	9422.95 ± 1003.02**	36.31 ± 3.37**

[a] A = Angus, B = Brahman

[b] Angus additive genetic effects are expressed as deviations from Brahman

[c] A x B intralocus nonadditive genetic effects are defined as deviations from those of the parental breeds

**P <.01

*P <.05

The direct nonadditive genetic effects accounted for 38.3%, 35.1% and 35.1% of the total genetic effects for WNa, WK and WW. Thus, WK followed the pattern shown by WW better than WNa.

The intrabreed intralocus interactions for the maternal nonadditive genetic effects were significant ($P<.01$) and about one and a half times larger than the direct nonadditive genetic effects (9422.95 ± 1003.02 mg WNa, 550.72 ± 114.44 mg WK and 36.31 ± 3.37 kg WW). This indicates that calves produced by A x B crossbred dams had higher amounts of WNa, and WK and larger WW than those produced by A and B straightbred dams. Reynolds et al. (1978) reported that A x B crossbred dams produce substantially higher milk yields than straightbred A and B dams. Thus, the large WNa, WK and WW realized might have partly been attributed to larger milk yields from crossbred dams. Nonadditive maternal genetic effects accounted for 60.8, 63.5, 64.0 % of the total genetic effects for WNa, WK and WW. Thus, the trend of WK and WW was similar.

The similarity of response of WK and WW for all genetic effects in this study could be attributed to the physiological link that exists between K and growth. The elongation process of protein synthesis in which amino acids are esterified to the corresponding transfer RNA requires K (Lewin, 1970). Potassium also activates the activity of glutamylcysteine synthetase enzyme to produce glutamylcysteine which is used in the synthesis of glutathione that is required for synthesis of amino acids (White et al., 1973). On the other hand, Na is a constituent of the enzyme Na, K-ATPase which activates DNA synthesis that is essential for cell growth and differentiation (Lingrel et al., 1990; Kaplan, 1978). Thus, the similar response between WNa and WW might exist because of this metabolic relationship that exists between Na and growth. Similarities between WK and WNa which were also observed in this study. This suggests that the functions of K and Na might be related. This observation supports the findings of Sanchez (1992) in Central Florida who reported K and Na to perform some of the same functions. Underwood (1981) also reported that K can meet the needs of Na. The large nonadditive genetic effects realized in all the traits suggest that the: 1) alleles for WNa, WK and WW are different in A and B breeds, 2) alleles in A and B breeds differ in frequency in these traits, and 3) favorable alleles for these traits exhibit nonadditive gene action. It is generally also recognized that the A breed is not well adapted in the southern region of U.S. The B breed also is somewhat unadapted to the region since the climatic conditions are not as tropical as the region where B originally evolved (the cattle used to develop the B breed in the U.S were largely from Brazil, Sanders, 1980). It is plausible that heterosis might be optimized in an intermediate environment (subtropical) which would be more suitable for the crossbred animals but would not be perfectly suitable for either of the two parental breeds.

Combining Ability of Sire and Dam Breed Groups

The combining abilities (Table 14) are the total of additive and nonadditive genetic effects of using sires of different breed groups in the multibreed herd of A and B breeds and their crosses.

Irrespective of the breed group of sire mated to, calves from F_1 dams had the largest amount of serum WNa and WK and highest WW. This result was due of the large nonadditive maternal genetic effect obtained in the F_1 dams. The largest amount of WNa and WK and highest WW were obtained in calves when B sires were mated to F_1 dams (12,400 ± 1113.28 mg WNa, 703.41 ± 127.02 mg WK and 46.34 ± 3.74 kg WW). This was due to: 1) the extremely large nonadditive A x B maternal genetic effect expressed by F_1 dams (100% maternal heterosis), and 2) large A x B nonadditive direct genetic effect (representing 50% individual heterosis) of calves from F_1 dams. Except for the mating of A sires to .25A.75B dams, calves from .5A.5B (F_2) dams had the second largest amount of serum WNa and WK and highest WW when mated to all breed groups of sire. This was due to the same reasons for F_1 dams. Calves from the mating of A sires x A dams had the lowest combining ability. This was a result of the large negative value for direct additive genetic effects (-216.70 mg WNa, -23.16 mg WK, -.74 kg WW) and low positive additive maternal genetic effects (131.79 mg WNa, 12.37 mg WK, .51 kg WW).

TABLE 14. COMBINING ABILITY OF SIRE BREED GROUPS MATED ACROSS DAM BREED GROUPS FOR SERUM POTASSIUM, AND SODIUM AND WEIGHT AT WEANING

Breed group of dam[1]	Trait[2]	Breed group of sire[1]				
		Angus	.75A.25B	.5A.5B	.25A.75B	Brahman
Angus	WK	-10.79 ± 4.87*	68.25 ± 36.75	147.29 ± 73.06*	226.33 ± 109.48*	305.37 ± 145.92*
	WNe	-84.91 ± 42.74*	1425.09 ± 322.10**	2935.09 ± 640.32**	4445.09 ± 959.48*	5955.09 ± 1278.89**
	WW	-.23 ± .14	4.84 ± 1.08**	9.91 ± 2.15**	14.98 ± 3.23**	20.06 ± 4.30**
.75A.25B	WK	271.68 ± 52.39**	312.64 ± 64.78**	353.61 ± 79.45**	394.58 ± 95.35*	435.55 ± 111.95*
	WNe	4925.75 ± 15.92**	5694.30 ± 567.75**	6462.83 ± 696.29**	7231.38 ± 835.63**	7999.93 ± 981.19*
	WW	18.33 ± 1.54**	20.91 ± 1.91**	23.49 ± 2.34**	26.08 ± 2.81**	28.66 ± 3.30**
.5A.5B(F$_1$)	WK	691.83 ± 127.01**	694.72 ± 127.01**	697.62 ± 127.01**	700.51 ± 127.01**	703.41 ± 127.02**
	WNa	12292.15 ± 1113.18**	12319.24 ± 38.60**	12346.33 ± 1113.12**	12373.41 ± 1113.17**	12400.50 ± 1113.28**
	WW	45.96 ± 3.74**	46.06 ± 1.91**	46.15 ± 3.74**	46.25 ± 3.74**	46.34 ± 3.74**
.5A.5B(F$_2$)	WK	416.47 ± 86.48**	419.36 ± 86.43**	422.26 ± 86.39**	425.15 ± 86.36**	428.05 ± 86.34**
	WNe	7580.68 ± 757.97**	7607.76 ± 757.53**	7634.85 ± 757.18**	7661.94 ± 756.91**	7689.03 ± 756.72**
	WW	27.81 ± 2.55**	27.90 ± 2.55**	28.00 ± 2.55**	28.09 ± 2.55**	28.18 ± 2.55**
.25A.75B	WK	423.57 ± 112.31**	388.40 ± 95.58**	353.22 ± 79.57**	318.04 ± 64.81**	282.86 ± 52.38**
	WNa	7879.86 ± 984.30**	7165.49 ± 837.67**	6451.12 ± 697.35**	5736.75 ± 568.03**	5022.38 ± 459.11**
	WW	28.21 ± 3.31**	25.82 ± 2.82**	23.42 ± 2.35**	21.03 ± 1.91**	18.63 ± 1.54**
Brahman	WK	293.00 ± 146.44	219.75 ± 109.83*	146.50 ± 73.22*	73.25 ± 36.61*	0
	WNe	5823.31 ± 1283.40	4367.48 ± 962.55**	2911.66 ± 641.70**	1455.83 ± 320.85**	0
	WW	19.54 ± 4.32**	14.66 ± 3.24**	9.77 ± 2.16**	4.89 ± 1.08**	0

[1] A = Angus, B = Brahman.

[2] Total genetic values for WCe, WP and WMg are expressed in mg, and for WW in kg.

**P < .01

There was a consistent increase in WNa, WK and WW in calves as the proportion of B increased in the breed group of sire. This was a result of 1) high additive genetic values of WNa, WK and WW in B sires (-108.35 ± 31.84 mg WNa, -11.58 ± 3.63 mg WK and -.38 ± .11 kg WW), and 2) higher A x B nonadditive genetic values of WNa, WK and WW in calves from A and crossbred A x B dams sired by B bulls. Thus, the B bulls were superior in both additive genetic and total genetic values (additive plus nonadditive).

The B x A calves excelled over A x B calves in all the three traits indicating that reciprocal differences were important. The advantage of B x A calves in WW found in this study concurred with the results of the studies done by Turner (1969) in Louisiana and Long et al. (1980) in Texas.

CHAPTER SIX

HERITABILITIES OF AND GENETIC,ENVIRONMENTAL AND PHENOTYPIC CORRELATIONS AMONG SERUM POTASSIUM AND SODIUM AND WEIGHT AT WEANING IN AN ANGUS BRAHMAN MULTIBREED HERD

Introduction

Sodium (Na) and potassium (K) are essential elements in animals. They are involved in osmotic balance, acid base regulation and water balance (Underwood, 1981). Potassium also is involved in ionic balance controlling cellular excitability and activation of several enzyme systems (Underwood, 1981), including that of amino acid chain elongation during protein synthesis (Lewin, 1970). Increased K also causes release of insulin (Church, 1988) which is a growth factor for cells (Darnell, 1990). In ruminants Na neutralizes acidic compounds produced by rumen fermentation (Payne and Payne, 1987). Both K and Na are constituents of milk (Underwood, 1981; Beede et al., 1983) and thus are available to calves through their dams.

Sodium supplementation of grazing beef cattle in the form of common salt (sodium chloride) is a widely accepted practice in most countries (Minson, 1990); however, both K and Na also are critical in tropical countries because of higher loss of these elements in sweat (Underwood, 1981; Beede et al., 1983; McDowell et al., 1983). Furthermore, under heat stress conditions such as experienced in subtropical and tropical conditions, homeostatic mechanisms attempt to maintain body temperature by reducing feed consumption (McDowell, 1972); consequently, intake of essential nutrients including K and Na can be reduced. Potassium and Na may be important under these conditions since they are major regulators of water balance (Vander, 1980).

Supplementation of K and Na is limited in tropical and subtopical developing countries because of exorbitant cost and/or unavailability. Thus, losses due to deficiencies of these elements are more pronounced in tropical and subtropical countries relative to temperate countries.

Frequently salt is used as a regulator of intake of supplements provided free choice to animals on range. Strategic placement of salt or salt meal mixture on range also is purported to give better distribution of grazing.

Weaning weight (WW) is an important selection criterion in beef animals because it reflects the preweaning growth of the calf. It also is moderately inherited and has moderate to high genetic correlation with postweaning weight and carcass traits. Thus, genetic improvement of WW is necessary. Genetic improvement of WW is influenced among other factors by heritability of the trait and by genetic, environmental and phenotypic correlations with correlated traits. Traits correlated with WW can increase accuracy of selection for WW, thus enabling genetic progress of WW to increase.

Despite the nutritional and physiological significance of K and Na macrominerals, there are apparently no genetic studies that relate them to growth. Thus, objectives of this study were:

i. to estimate heritabilities of amounts of serum K and Na at weaning and WW and

ii. to estimate additive genetic, environmental and phenotypic correlations among K and Na at weaning and WW.

Materials and Methods

Animals

In two years of research, 1989 and 1990, six herds of cows representing a multibreed herd was maintained. The herds were composed of: 65, 76, 18, 38 and 46 cows representing Angus (A), Brahman (B), .75A.25B, .5A.5B and Brangus, respectively. Paternal half sibs were produced by mating all the six breed group of sires across breed groups of dams in a diallel type of mating . The animals were located at Pine Acres Research Center, Citra, Florida. The 243 cows ranged between 3 and 8 years of age. They were bred artificially (in March for A and AxB dams and April for B dams) following estrus synchronization with prostaglandin $F_{2\alpha}$ and subsequently assigned to six clean up herds for 60 days with one bull representing each breed group. Connectedness across years and herds was created by assigning at least one bull from each breed group to sire calves in both years. In the two years, the largest number of sires (Table 15) were from purebred sires (7 for Brangus, 5 for B and 5 for A). Correspondingly, the largest number of progeny were from the purebred sires (92 for B, 85 for Brangus and 66 for A).

The six cow herds were maintained on bahiagrass pastures (Paspalum notatum) with a complete free choice mineral supplement containing 20% calcium, 9% phosphorus, .25% magnesium, 6.12% sodium and 18.18% chlorine. In winter and early spring (Mid-December to March), the dams were assigned to six replicated forage supplementation regimens and a control herd. The diet consisted of molasses and bermudagrass (Cynodon dactylon) hay fortified with urea (32% Nitrogen).

Records

Blood was taken from a total of 380 calves and serum was extracted from it. Weight at weaning (WW) was measured concurrently with blood sampling. Since colostrum was not of interest, the first blood sample was taken after about 7 days postpartum. Mineral concentrations of K and Na were determined from solutions made from serum (Fick et al., 1979). The atomic absorption spectrophotometry method was used to determine the mineral concentrations. All calves were weaned at approximately 7 months of age.

TABLE 15. DISTRIBUTION OF SIRES AND CALVES BY BREED GROUP OF SIRE

Breed[a] group	Number of sires	Number of calves 1988	1989	per sire	Total
A	5	38	28	13.2	66
.75A.25B	3	26	25	17.0	51
.5A.5B	4	8	23	7.8	31
.25A.75B	4	29	26	13.8	55
B	5	46	46	18.4	92
Brangus	7	44	41	12.1	85
Total or average	28	191	189	13.6	380

[a] A = Angus, B = Brahman

The records were adjusted to 205 days using the Beef Improvement Federation (BIF, 1990) recommendations. Concentrations of K and Na of the first samples were taken to represent those at birth since no samples were taken at birth. The amounts of these minerals were estimated as a product of estimated serum volume and concentration. Serum volume was estimated as a product of the weight of the calf, expected fraction of blood in cattle relative to weight (.077; Frandson, 1975) and expected fraction of serum in blood relative to blood volume (.6; Jesse, 1979).

Estimation of Variances, Covariances and Heritability

Estimates of variances and covariances were obtained using the restricted maximum likelihood (REML) method (Patterson and Thompson, 1971; Corbeil and Searle, 1976). Variance components procedure, single trait option, (SAS, 1985) was used for computation. Dependent variables included amount of K at weaning (WK) , amount of Na at weaning (WNa) and weight at weaning (WW). The mixed model contained fixed group environmental effects including: year of birth of calf, winter management within year, age at initial sampling after birth, sex, age of dam and interaction of sex and age of dam. Fixed genetic effects also included the interactions of breed group of sire and breed group of dam and those of breed group of maternal grandsire by breed group of maternal grandam. Random effects were sire within breed group of sire and residual. All the sires were unrelated except two that were half sibs.

Fixed effects were assumed to have mean zero, common variance and to be uncorrelated. Assuming that sire differences are entirely genetic, variances of sires (σ^2_s) within sire groups represents .25 additive direct genetic variance (σ^2_A). That is $\sigma^2_A = 4\sigma^2_s$. This σ^2_A represents the component of variance for half sibs. The residual variance (σ^2_R) represented .75 additive direct genetic variance, additive maternal genetic variance and nonadditive (direct and maternal) genetic variances, covariances between direct and maternal genetic effects and variances due to random environmental effects (σ^2_E) . Thus, σ^2_E was computed as: $\sigma^2_R - 3\sigma^2_s$.

Covariances were estimated for additive genetic, phenotypic and environmental components using a linear function of the variance of the sum of two traits (X, Y) and the variance of the individual traits (Searle and Rounsaville, 1974). Thus, the covariance of traits X and Y = .5[Var (X + Y)] - .5Var X - .5Var Y since Var (X + Y) = Var X + Var Y + 2Cov (X, Y). Thus, REML estimates of sire and residual components of variance were estimated as the sum of all possible pairs of traits (WNa + WK, WNa + WW, WK + WW). Environmental covariances were computed as the difference between residual covariance and three times the sire covariance, whereas phenotypic covariance was estimated as a sum of sire and residual covariances. The genetic, environmental and phenotypic correlations were computed as a ratio of the covariance of the traits to that of the square root of the product of the variance of the individual traits.

Results and Discussion

Restricted maximum likelihood estimates of variance components for WK, WNa and WW are shown in Table 16. Sire variance estimate for WW was 34.76 ± 25.00 kg^2. Thus, variation of WW due to sire was small. The estimate was within (21 to 52 kg^2) that reported by Kennedy and Henderson (1975) for the Angus. Residual variance of WW for 363.92 ± 32.11 kg^2 also was close to the 381 to 395 kg^2 reported by Kennedy and Henderson (1975) in Angus. The variance component due to sire for WK was large (11210.64 ± 21710.57 mg^2) but with a corresponding large standard error. The sire variance component for WNa was large with a smaller standard error (4209818.49 ± 2614974.72 kg^2) relative to that of WW and WK. The residual variances for WK and WNa were large with small standard errors (470293.06 ± 41545.17 mg^2 for WK, 32323947.63 ± 285633.99 mg^2 for WNa). The sire variance was relatively smaller than residual variance and accounted for only 2.33%, 11.52% and 8.72% of total variation in WK, WNa and WW respectively. No estimates of variance components for WK and WNa were found in the literature. Residual variances were estimated with higher accuracy than sire variances in all the traits. The type of feed on which the animals were maintained might have not been good enough to produce maximum milk production and thus enable calves to express more fully their genetic potential.

Heritability estimates (h^2) for WK, WNa and WW are presented in Table 17. The estimates were .09 for WK, .46 for WNa and .34 for WW.

TABLE 16. RESTRICTED MAXIMUM LIKELIHOOD ESTIMATES OF VARIANCE COMPONENTS FOR SERUM POTASSIUM AND SODIUM AND WEIGHT AT WEANING

	Variance component estimates[2]	
Trait[1]	Sire	Residual
WK	11210.64 ± 21710.57	470293.06 ± 41545.17
WNa	4209818.49 ± 2614974.72	32323947.63 ± 2856337.99
WW	34.76 ± 25.00	363.92 ± 32.11
WK + WNa	4693832.00 ± 95083.55	37928651.97 ± 33528.64
WK + WW	12673.95 ± 22960.23	486523.80 ± 42996.45
WNa + WW	4235060.60 ± 83184.52	32509670.02 ± 90844.85

[1] WK, WNa, WW = serum K, and weight at weaning.

[2] Estimates of variance components are expressed in mg^2 for WK and WNa, in kg^2 for WW, in (mg + mg)^2 for sums of macromineral traits and in (mg + kg)^2 for sums of macromineral traits and WW.

The estimate for WW agreed with those reported in the literature (.37; .4; .44; .25; Nelsen and Kress, 1979; Schaeffer and Wilton, 1981; Kennedy and Henderson, 1975; Bertrand and Benyshek, 1987). The low h^2 for WK indicates that the trait cannot be improved by selection based on individual's records. On the other hand, the moderate h^2 estimates of WNa and WW indicate that selection based on the individual's record could improve these traits. Improved efficiency in utilization of WNa would be advantageous in deficiency situations and in tropical and subtropical areas because of heat stress that results in increased loss of endogenous Na (Underwood, 1981). The low h^2 estimate of WK (.09) confirms the property of K to be susceptible to environmental influences. For instance, hemolysis frequently occurs as a result of leakage of K from the erythrocytes during separation of serum from hematocrit.

Estimates of genetic, environmental and phenotypic correlations between WK, WNa and WW are presented in Table 17. Genetic correlation between WK and WNa was high, above unity and positive (1.03). This possibly was because of random errors associated with the few number of sires and corresponding few progeny per sire (Table 15).

However, the high positive genetic correlation indicates that many of the same alleles that affect WK also affect WNa. This observation is supported by the physiological functions that K and Na jointly perform. For instance, both

TABLE 17. ESTIMATES OF HERITABILITIES (±SE) AND GENETIC (±SE), ENVIRONMENTAL AND PHENOTYPIC CORRELATIONS AMONG SERUM POTASSIUM AND SODIUM AND WEIGHT AT WEANING

Trait[2]	WK	WNa	WW
WK	.09 ± .10	1.03 ± NE	.94 ± .06
WNa	.65 (.67)	.46 ± .18	.94 ± .04
WW	.59 (.62)	.84 (.87)	.35 ± .16

[1] Heritabilities on the diagonal; genetic correlations above the diagonal; environmental and phenotypic (in parenthesis) correlations below the diagonal.

[2] WK, WNa, WW = Serum K, Na and weight at weaning.

NE = Not estimable.

minerals function in maintaining acid-base and osmotic balances within the animal cells (Underwood, 1981; Minson, 1990). During deficiency of Na, K can replace Na (Underwood, 1981). This occurs as a result of increased secretion of aldosterone hormone by the adrenal glands and an increase in the sensitivity of the parotid glands (Underwood, 1981). Sodium is required by the kidney for K conservation and to balance bicarbonate excretion (Vander, 1980). The transport of Na and K ions across the cell membrane also is catalyzed by one enzyme, Na, K ATPase (Darnell et al., 1990). The transfer of these ions is stimulated by insulin (White et al., 1968). The synthesis of this enzyme is induced by aldosterone in combination with triiodothyronine (Morel and Doucet, 1986). The action of aldosterone requires the presence of thyroid hormone (Morel and Doucet, 1986). In rats glucocorticoids have been shown to sustain Na, K ATPase activity by inducing the synthesis of lipocortin (Morel and Doucet, 1986), a protein that inhibits phosphorylase A_2 (Reeds, 1989). Arachidonic acid then is released, stimulating production of prostaglandin $F_{2\alpha}$ and E_2, which are proposed to effect protein phosphorylation. This process results in protein accretion and dephosphorylation which in turn results in protein degradation (Reeds, 1989). It is plausible that aldosterone, triiodothyronine, glucocorticoid and insulin hormones have pleiotropic effects on K and Na. All these processes of metabolism of K and Na suggest that many of the same alleles that influence serum WK also influence serum WNa.

Genetic correlations between WK and WW (.94) and between WNa and WW (.94) were high suggesting that many of the same alleles that affect WK and WNa also affect WW positively. This magnitude of genetic correlation between WK and WW and between WNa and WW support the physiological link that exists between these minerals and growth. Potassium activates chain elongation during protein synthesis (Lewin, 1970). Linderman and Pederson (1983) and Durand and Kawashima (1980) also have reported that K is required for protein synthesis. Potassium also activates pyruvate kinase which catalyses carbohydrate synthesis (Lehninger, 1984). Insulin promotes: i) the conversion of carbohydrates into triacylglycerol, ii) amino acid uptake by muscle cells, iii) ribosome aggregation as polyribosomes, iv) aminoacyl-tRNA binding to ribosomes and v) the number and activity of ribosomes (Beitz, 1985). Thus, K may be contributing to growth through protein and fat synthesis and this might be the basis of high genetic correlation between WK and WW. On the other hand, Na is essential for cellular uptake of glucose through activation of the glucose carrier protein (NRC, 1984). The carrier protein must bind Na ions in order to bind glucose (White et al., 1968). Thus, the presence of Na may be a rate limiting factor in carbohydrate metabolism which in turn may limit growth. Lingrel et al. (1990) reported that increased intracellular Na stimulates Na, K-ATPase activity whereas Vandenburgh and Kaufman (1981) observed that Na, K-ATPase is one of the initiating events associated with stretch induced protein synthesis. Similarly, it has been observed that in cultured fibroblasts, lymphocytes and neuroblastoma cells that Na, K-ATPase activates deoxyribonucleic acid synthesis and cell hyperplasia (Kaplan, 1978; Rozengurt and Mendoza, 1980; Mummery et al., 1981). Thus, the high genetic correlation between WNa and WW may be through these physiological processes.

The high positive genetic correlations between these mineral traits and WW suggest that it might be possible to have animals that need lower amounts of WK and WNa to achieve the same weaning weight. Thus, a possible selection criterion could be to select calves with higher efficiency of WK and WNa utilization to achieve the same weaning weight. These would be animals with lower WK and WNa requirements and larger WW. This approach would take advantage of the animal's physiological homeostatic mechanism by resulting in an increase in aldosterone secretion which would reduce the amount of K and Na excreted. However, little genetic change would be expected from selecting animals with low WK since WK has low h^2. Thus, more emphasis would be placed on WNa than WK. Since Na also is involved in carbohydrate synthesis which can be metabolized into fatty acids, single trait selection for WNa might increase fat deposition. A study by Evans (1954) elucidated this. In this study, fat tailed Lebanese sheep were found to have higher levels of K and Na than Merino sheep which are not fat tailed. Thus, selection for moderate amount of WNa may play an important role in energy conservation through storing energy reserves as fat when feed is abundant and mobilizing fat to supply energy in times of energy shortage. This selection procedure would be particularly advantageous in very extensive grazing conditions similar to those experienced in most tropical areas.

Estimates of environmental correlations among all the traits were high and positive. The values were .65 for WK and WNa which suggests that WK responds to many of the same environmental factors in a similar manner as WNa. The environmental correlation between WK and WW was .59 and that between WNa and WW was .84. Thus, WK and WNa respond to many of the same environmental factors affecting WW. These high environmental correlations might have been attributed to common environmental factors affecting all the three traits. For example, a decrease in feed intake due to nutritional changes might decrease thyroid hormone function which in turn would reduce the activity of Na, K-ATPase (Lingrel et al., 1990), thus resulting into reduced WK and WNa. Reduced activity of Na, K-ATPase would result in decreased energy available for metabolism (Beitz, 1985) , thus reducing WW. Similarly, decreased protein intake would decrease insulin production which would impair glucose utilization resulting in less pyruvate being converted to acetyl coA. This would result in less fatty acid synthesis which would in turn result in reduced WW. A decrease in insulin would result also in decreased Na, K-ATPase activity (Lingrel et al., 1990). Differences in milk yield which may be higher in crossbred A x B dams relative to straightbred dams may result also in a high environmental effect because of larger quantities of milk and amount of K and Na that would be available to the calf.

Phenotypic correlations between the mineral traits and those between the mineral traits and WW also were high and positive. The values were .67 between WK and WNa, and .62 between WK and WW and .87 between WNa and WW. Thus, selection on phenotypic value for any one trait will result in a correlated phenotypic increase in the other traits.

CHAPTER SEVEN
SUMMARY AND CONCLUSIONS

Four studies were conducted at Pine Acres Research Station, Citra, Florida, to study the environmental and genetic factors affecting calcium, phosphorus, magnesium, potassium and sodium macrominerals and their relationships with preweaning growth in an Angus-Brahman multibreed herd.

Calves were produced by mating Angus, Brahman, 75% Angus 25% Brahman, 50% Angus 50% Brahman, 25% Angus 75% Brahman and Brangus (63% Angus 37% Brahman) sires to dams of the same expected breed fractions, except 25% Angus 75% Brahman dams. There were a total of 380 calves in two years (1989 and 1990) from which birth weight, weight at weaning, blood samples near birth and blood samples at weaning were taken. Serum was extracted from the blood samples by centrifuging at 700 g for 30 minutes. The amount of each macromineral was computed as the product of the concentration times the estimated serum volume of each calf. Serum volumes were computed as the product of calf weights times the expected fraction of blood in cattle (.077) times the expected fraction of serum in blood (.6). All traits were projected to 205 days using the formula recommended by the Beef Improvement Federation.

In the first study, serum was deproteinized using 10% trichloracetic acid. A serum sample of 1 milliliter was diluted to 10 milliliters in deionized water. Serum concentrations of inorganic calcium and magnesium were then determined with the flame spectrophotometer. Concentration of phosphorus in the serum was determined by colorimetry. All concentrations were read against standard solutions.

The objective of the first study was to estimate additive and nonadditive genetic effects for calcium, phosphorus and magnesium and weight at weaning in an Angus-Brahman multibreed herd. The variables in the model included year of birth of calf, winter management, clean up herd within year, age of calf at first sampling after birth, sex, age of dam, and sex x age of dam interaction as fixed environmental effects. The genetic fixed effects were regressions on: Angus sire additive, Angus dam additive, Angus x Brahman direct nonadditive and Angus x Brahman dam nonadditive. Residual effects were assumed to be random.

Year and sex of calf were the only environmental effects important for all four traits ($P<.01$). Age of dam was only important for phosphorus and magnesium ($P<.01$). The interaction between sex x age of dam was important for magnesium ($P<.01$) and weight at weaning ($P<.04$). Winter management was important for calcium and weight at weaning ($P<.01$). Angus sire additive genetic effects were small but significant. The BLUE were -4.70 ± 1.25, -3.00 ± 1.10, and -.87 ± .27 mg for calcium, phosphorus and magnesium, respectively. The BLUE for weight at weaning was -.38 ± .11 kg ($P<.01$). The BLUE for Angus dam additive was not significant for calcium (1.86 ± 1.28 mg) and weight at weaning (.14 ± .11 kg), but was significant ($P < .01$) for phosphorus (-11.82 ± 1.13 mg) and magnesium (.83 ± .28 mg). The nonadditive direct genetic effects were large and significant ($P < .01$) for calcium (213.51 ± 50.20 mg), magnesium (48.26 ± 10.91 mg) and weight at weaning (19.91 ± 4.31 kg) but were not significant for phosphorus. Nonadditive maternal genetic effects were significant ($P < .01$) and much larger than direct nonadditive effects. The BLUE were 366.56 ± 39.32 mg for calcium, 95.50 ± 34.79 mg for phosphorus, 70.20 ± 8.54 mg for magnesium and 36.31 ± 3.37 kg for weight at weaning. The best combination was achieved by mating Brahman sires to 50% Angus 50% Brahman (F_1) dams (474.24 ± 43.64 mg calcium, 130.18 ± 38.61 mg phosphorus, 94.74 ± 9.48 mg magnesium and 46.34 ± 3.74 kg weight at weaning), while the worst was by mating Angus sires to Angus dams (-2.83 ± 1.68 mg for calcium, -14.82 ± 1.48 mg for phosphorus -.04 ± .36 mg for magnesium and -.23 ± .14 kg for weight at weaning).

Of all the genetic effects, nonadditive genetic effects (especially maternal) influenced the rankings of the sire breed group x dam breed group combinations the most. Thus, nonadditive genetic effects should be included in mixed models to predict genetic values of the progeny of animals involved in specific interbreed matings for amounts of macrominerals in serum and (or) weaning weight.

In the second study, heritabilities of and genetic, environmental and phenotypic correlations among serum calcium, phosphorus and magnesium and weight at weaning were estimated. The mixed model used contained year of birth of calf, clean up herd within year, age of calf at first sampling after birth, sex of calf, age of dam and sex x age of dam interaction as environmental effects, breed group of sire x breed group of dam interaction and breed group of maternal grandsire x breed group of maternal grandam interaction and sire within breed group of sire as genetic effects and residual. All effects were assumed fixed except sire and residual which were assumed random. Restricted maximum likelihood procedures were used to compute variance and covariance components.

The estimates of heritability were .39 ± .17, .40 ± .17, .36 ± .16, and .35 ± .16 for calcium, phosphorus, magnesium and weight at weaning respectively. The genetic correlations were .66 ± .17 for calcium and phosphorus, .70 ± .16 for calcium and magnesium, 1.00 for calcium and weight at weaning, .50 ± .23 for phosphorus and magnesium, .78 ± .12 for phosphorus and weight at weaning and .86 ± .08 for magnesium and weight at weaning. Environmental correlations were .55 for calcium and phosphorus, .71 for calcium and magnesium, .88 for calcium and weight at weaning, .51 for phosphorus and magnesium, .60 for phosphorus and weight at weaning and

.73 for magnesium and weight at weaning. Phenotypic correlations were .57 for calcium and phosphorus, .70 for calcium and magnesium, .88 for calcium and weight at weaning, .51 for magnesium and phosphorus, .63 for phosphorus and weight at weaning and .73 for magnesium and weight at weaning.

In the third study the deproteinized serum in the first study was diluted to 1 to 100 for potassium and 1 to 1000 for sodium with deionized water. The concentrations were read against standard solutions using the flame spectrophotometry method. The model was the same as in the first study. The purpose of the study was to estimate additive and nonadditive genetic effects of serum potassium and sodium and weight at weaning.

Year and sex were important environmental effects ($P < .01$) for all the three traits. Clean up herd was important for sodium ($P < .05$) and weight at weaning ($P < .08$). Age of dam was important for sodium ($P < .03$) and weight at weaning ($P < .09$). Winter management was important for sodium ($P < .01$) and weight at weaning ($P<.01$). Sex x age of dam interaction was important for sodium ($P < .07$) and weight at weaning ($P<.04$). The Angus sire additive genetic effects were negative and significant for all the three traits. The values were -11.58 ± 3.63 and -108.35 ± 31.84 mg for potassium and sodium respectively, and -.38 ± .11 for weight at weaning. The Angus dam additive values were not significant. The BLUE for A x B direct nonadditive genetic effects were large and significant ($P < .01$). The values were 304.58 ± 146.11 mg and 5931.66 ± 1280.58 mg for potassium and sodium respectively, and 19.91 ± 4.31 kg for weight at weaning. The nonadditive maternal effect was at least one and a half times larger than that of direct nonadditive effect. The values were 550.72 ± 14.44 and 9422.95 ± 1003.02 mg for potassium and sodium respectively, and 36.31 ± 3.37 kg for weight at weaning. Irrespective of the breed group of sire mated to, calves from F_1 dams had the largest amount of serum potassium and sodium and highest weight at weaning. The largest amount of potassium and sodium were obtained when Brahman bulls were mated to F_1 dams (703.41 ± 127.02 mg potassium, 12400 ± 113.28 mg sodium and 46.34 ± 3.74 kg weight at weaning). There was a consistent increase in amount of potassium and sodium and weight at weaning in calves as the proportion of Brahman increased in the sire. The lowest combining ability was obtained when Angus were straightbred (-10.79 ± 4.87 mg for potassium, -84.91 ± 42.74 mg for sodium and -.23 ± .14 kg for weight at weaning).

In the fourth study, heritabilities of and genetic, environmental and phenotypic correlations among potassium and sodium and weight at weaning were estimated. The model was the same as that of the second study.

The estimates of heritabilities were .09 ± .10 for potassium, .46 ± .18 for sodium and .35 ± .16 for weight at weaning. The estimates of genetic, environmental and phenotypic correlations were 1.03, .65, .67 (for potassium and sodium), .94, .59, .62 (for potassium and weight at weaning) and .94, .84, .87 (for sodium and weight at weaning).

The response of these macrominerals to environmental effects indicate that environmental effects on these macrominerals among themselves were not uniform similar. This is further elucidated by the environmental correlations among the macrominerals which ranged between .51 (phosphorus and magnesium) and .71 (calcium and magnesium).

The Angus sire additive genetic effects were small and negative but significant for all the traits; thus, the use of Brahman sires would tend to optimize these macromineral and weight at weaning traits in a crossbreeding system involving Angus and Brahman. Similarly because the Angus dam additive effect was negative for phosphorus but positive for magnesium, use of Brahman dams would be more suitable than use of Angus dams in a crossbreeding system involving Angus and Brahman. However, Angus dams would be more suitable for serum magnesium.

Crossbred calves had more of the serum macrominerals and were heavier at weaning than those from the straightbreds. This suggests that Angus and Brahman differ in the frequencies of the genes affecting efficiency of utilization of these macrominerals and weight at weaning or that the two breeds have different sets of alleles affecting these traits and that the traits are affected by nonadditive gene action. These differences in efficiency of utilization of K and Na might be in variation of grazing habits leading to differences in intakes of the minerals and differences in digestibility and absorption of the minerals.

Calves from crossbred dams had the most amount of macrominerals and weight at weaning relative to those from straightbreds. Thus, nonadditive maternal genetic effects were important and should be considered in planning subsequent crossbreeding programs involving Angus and Brahman.

For selection and evaluation of sire breed group combination with dam breed group that will yield maximum amount of the macrominerals and weight at weaning for each calf weaned, simultaneous consideration of direct and maternal additive effects and nonadditive effects are important. In this study, the mating of Brahman sires to .5A.5B (F_1) dams produced calves with the largest amount of macrominerals and heaviest weight at weaning. The worst calves were those of straightbred Angus mating.

The heritability estimates for all the traits were moderate to high except potassium which was near zero indicating that there is a sizeable amount of genetic variation in all these traits except potassium. As for potassium, the additive genetic variance was low with a large standard error; hence the heritability estimate for the trait was essentially zero. However, crossbred calves and calves from crossbred dams had larger amounts of potassium than those from straightbred dams. Thus, the superiority of these crossbred calves and those from crossbred dams was due to large nonadditive genetic variance. This suggests that improvement of potassium may be achieved mostly by crossbreeding. Thus, these serum macrominerals except potassium are heritable traits and are nearly as heritable as weight at weaning. This magnitude of heritabilities of the macrominerals, except that of potassium, may indicate that there is genetic variation in one or more of digestibility or absorption or excretion which could be utilized in obtaining efficiency of utilization of these macrominerals through selection. The improved efficiency of utilization of these dietary minerals should be advantageous in deficiency situations where the animals respond to supplementary minerals. Management also could be geared to meet the genetic needs of animals in order to reduce the risks of deficiency. However, genetic improvement by way of selection for the macrominerals should reduce the need for prophylactic measures in a cumulative and lasting ways.

The high genetic correlations between calcium, phosphorus and magnesium and weight at weaning indicate that improvement of calcium or phosphorus or magnesium would result in genetic improvement of the other traits. Likewise, potassium would be improved on indirectly if selection were for sodium, and vice versa. Improvement of these minerals also would result in a correlated improvement in weight at weaning. The moderate to high phenotypic correlations suggest that retaining calves with high weight at weaning also would result in having calves with high amounts of serum macrominerals. Selection should aim at combining high efficiency of macromineral utilization with high growth potential. To achieve this, selection would be for high weaning weights and low amounts of macrominerals in serum. However, because this may not be feasible, identification of animals that require lower amounts of calcium, phosphorus, magnesium and sodium for preweaning growth in a good nutritional environment might, in practice, be the first step for identification of animals capable of adequate growth and development under conditions of limited availability of these macrominerals. Semen, sires and/or dams where possible, with these characteristics could then be taken to areas with known deficiencies and progeny tested for these macrominerals. This assumes that weight at weaning and these macrominerals in the two environments are correlated traits. To determine whether selection in a good environment would produce animals which are superior in a poor environment, genetic correlation between the macrominerals and weight at weaning first is determined. Subsequently, correlated response in a poor environment to selection in a good environment is computed as a product of genetic correlation between the traits in good and poor environments, the square root of the heritability in the good and poor environments and the additive genetic standard deviation of the trait in poor environment (Falconer, 1981).

The equation to express the total amount of serum macromineral (Appendix) considered the relationship that exists among mass, volume and density (Mass = Volume x Density). Therefore blood weight (kg) = Blood volume (lt) x density (kg/lt). For blood weight (kg) to be equal to one, density of blood has to be one. Thus, it was inadvertently assumed that specific weight of blood is one. However, specific weight of blood is approximately

1.05 (Alman, 1961). If the 1.05 value were used rather than 1, the ratio of blood weight to blood volume would be 1.05. Thus, blood weight (kg) = 1.05 x blood volume (lt). In this case blood weight would be greater than blood volume by 5%. The consequence of assuming that the ratio of blood weight to blood volume is unity meant that the serum volume was overestimated by 5%. Subsequently, amount of each macromineral also was overestimated by 5%. However, the proportions 1:1.05 are close enough in magnitude to assume that they are the same. Thus, the assumption made in this research that the ratio of blood weight to blood volume is unity holds. The correlation (genetic and phenotypic) between blood volume and body weight was one. Thus, in calculating amount of each macromineral, the first equation that is a product of body weight and concentration yields the same result as the alternative one that is expressed as a product of blood volume and concentration (assuming the specific weight of blood is one). Thus, in retrospect we could have used the product of body weight and concentration to express amount of the macromineral as an alternative since it is more practical. There is also no difference in the coefficient used to arrive at serum volume because they cancel out in the equations. Thus, irrespective of the coefficient used the genetic parameters (heritability, genetic and phenotypic correlations) will not be affected.

Because macrominerals constitute the body tissues (e.g., muscle, bone, serum), they have a biological part-whole relationship with weight. Thus, the macromineral traits were expected to be correlated among themselves and with WW. Sharma et al. (1982) on the one hand showed that multiplying a random variable by a constituent percentage causes an inherent relationship between the random variable and the constituent trait. Thus, since total amount of serum macromineral traits were derived as a product of weight of animal, concentration of the macromineral in serum, proportion of blood to weight and proportion of serum to blood, mathematical relationships existed between the serum amount of macromineral traits and weight. As a consequence, estimates of genetic, environmental and phenotypic correlations were expected to be higher than they would have been had actual serum volume been used in determining amount of macromineral. However, it was not feasible to measure serum volume in this research, thus, the magnitude by which these genetic parameters were overestimated could not be quantified.

The next step in this research program would be to identify those animals that concurrently have high efficiency of utilization of these macrominerals and high weights at weaning and identify the alleles responsible for these traits. This would require the technical inputs from molecular biologists and animal geneticists. In this way we would be in a better position to explain genetic variation in this multibreed population.

Future studies also should look at interaction of these macrominerals and their relationship with weight at different ages and any other minerals (eg. Selenium, Cobalt) and blood metabolites that have been implicated in growth and development. Having predictions of genetic values of a large number of biological traits as well as weights will allow the selection of animals that will have much better defined nutritional requirements for growth.

Durand and Kawashima (1980) have indicated that these macrominerals are needed by rumen microbes for their normal functions. Thus, their deficiency may limit the production level through the rumen microbes. What is not clear is whether differences in rumen calcium, phosphorus, magnesium, potassium and sodium metabolism would affect their availability through diet.

Since absorption is one of the means by which efficiency of utilization of the minerals might be controlled, use of genetic engineering to impose control on mineral absorption might be considered. In this case, a gene involved in a rate limiting step of mineral absorption would be identified and controlled. On the other hand, genetic engineering procedures could be considered to find out if genes are responsible for rumen environment involving metabolism of the minerals, and hence, the availability of the dietary minerals at critical periods.

Finally, these studies have shown that serum calcium, phosphorus, magnesium and sodium are genetically, environmentally and phenotypically linked to weight at weaning. Thus, they can help identify animals that make more efficient use of these macrominerals for preweaning growth. They could be used together with other biological traits (which are involved in growth) in multiple trait selection programs to predict preweaning growth with high accuracy. However, since feed intake measurement was not feasible in this study, it is recommended that such measurements be taken in future studies to elucidate findings in this study.

APPENDIX

1. Total amount of serum macromineral

$$=$$

$$\left[\frac{Serum\ volume\ (lt)}{Blood\ volume\ (lt)}\right] \times \left[\frac{Blood\ weight\ (kg)}{Body\ weight\ (kg)}\right] \times \text{Body weight (kg)}$$

$$\times$$

$$\text{Concentration of macromineral (conc)}$$

$$\text{Concentration} = \frac{Macromineral\ amount\ (kg)}{Serum\ volume\ (lt)}$$

The equation for the amount of serum macromineral requires that the ratio of blood weight to blood volume is unity.

2. Correlations (r) (Genetic and/or Phenotypic)

a.i. Body weight (bwt) and serum macromineral amount (amt)

$^r(\text{bwt, amt}) = {}^r(\text{bwt, k} \times \text{bwt} \times \text{conc})$, where k is a constant.

$^r(\text{bwt, amt}) = {}^r(\text{bwt, k} \times \text{bwt} \times \text{conc})$

$$^r(\text{bwt, k} \times \text{bwt} \times \text{conc}) = \frac{k \times Cov\,(bwt,\ bwt \times conc)}{\left[Var\,(bwt) \times k^2 \times Var\,(bwt \times conc)\right]^{.5}}$$

$$= \frac{k\ Cov(bwt,\ bwt \times conc)}{k\,[Var(bwt) \times Var\,(bwt \times conc)]^{.5}}$$

$$= \frac{Cov(bwt,\ bwt \times conc)}{[Var(bwt) \times Var(bwt \times conc)]^{.5}}$$

ii. Blood volume (bldv) and serum macromineral amount (amt).

$$r(\text{bldv, amt}) = r(k \times \text{bwt}, k \times \text{bwt} \times \text{conc})$$

$$r(k \times \text{bwt}, k \times \text{bwt} \times \text{conc}) = \frac{Cov(k \times bwt, k \times bwt \times conc)}{[Var(bwt) \times k^2 \times k^2 \times Var(bwt \times conc)]^{.5}}$$

$$= \frac{k^2\ Cov(bwt, bwt \times conc)}{k^2[Var(bwt) \times Var(bwt \times conc)]^{.5}}$$

$$= \frac{Cov(bwt, bwt \times conc)}{[Var(bwt) \times Var(bwt \times conc)].5}$$

Thus, the correlations (genetic and phenotypic) of body weight and serum macromineral amount, and blood volume and serum macromineral amount are identical.

b. Blood volume (bldv) and body weight (bwt).

$$r(\text{bldv, bwt}) = r(k \times \text{bwt, bwt})$$

$$= \frac{k\ Cov(bwt, bwt)}{[k^2\ Var(bwt) \times Var(bwt)]^{.5}}$$

$$= \frac{k\ cov(bwt, bwt)}{k\,[Var(bwt) \times Var(bwt)]^{.5}}$$

$$= \frac{Var(bwt)}{Var(bwt)}$$

$$= 1$$

3. From 2b above serum macromineral amount can be expressed by two equations.

i. amt = bwt × conc

ii. amt = bldv × specific weight of blood × conc.

= bldv × conc since specific weight of blood was assumed to be unity.

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BIOGRAPHICAL SKETCH

William Ouko Odenya was born on January 9, 1952 in Kisumu district, Kenya. He graduated from Onjiko High School in December, 1970 and entered Egerton College, Njoro, Kenya where he was trained for three years for a diploma in range management. From January, 1974 to August, 1975 he was employed by the Ministry of Agriculture as an assistant research officer in sheep and goat breeding and management. In September, 1975 he was awarded a United Nations, Food and Agriculture Organization (F.A.O) fellowship to study for a Bachelor of Science degree in animal science at New Mexico State University, Las Cruces, New Mexico, U.S.A. In January, 1977 he returned to Kenya and continued working with the same employer until March, 1980 when he was awarded another F.A.O fellowship to study for a Master of Science degree in animal science at University of California, Davis, U.S.A. The title of his thesis which was based on data from Kenya was 'Relationship of coat cover and production traits in Dorper breed of sheep'. He completed his studies at UC, Davis in August, 1982, and returned to Kenya to work for the Ministry of Agriculture/F.A.O Sheep and Goat Development Project as a co-ordinator for sheep and goat breeding and management projects in the country. In July, 1984 he transferred his services to Egerton University as an instructor in animal science. In January, 1988 he was awarded a fellowship by Egerton University to study for a Doctor of Philosophy degree in animal science at the University of Florida, Gainesville, U.S.A. Upon completion of his studies in May, 1992, he will return to Kenya to resume teaching and research duties at Egerton University. The author is a member of Animal Production Society of Kenya and Farming Systems Society of U.S.A. He has served as Secretary of the Goat Breeders Society of Kenya.

The author is married to Jemimah Anyango and they together have three children: Daniel, Patricia and Erick.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

M. A. Elzo

Mauricio A. Elzo, Chairman
Assistant Professor of Animal Science

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Professor of Animal Science

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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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